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The subfamily Abbottellinae (Gastropoda: Annulariidae): origins, associations, and a review of the Hispaniolan taxa

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ABSTRACT

The subfamily Abbottellinae of the Annulariidae has been recognized as a speciose group in northern Hispaniola. This study, using phylogenetic (COI, 12S, H3), radular, and conchological characteristics, compared this group to other non-Hispaniolan annulariids to determine their wider associations and potential origin. Results indicate that the subfamily is related to the eastern Cuban *Annularisca* sensu lato and that genus should be moved to the Abbottellinae. The group dates from the time when eastern Cuba and northern Hispaniola were in close contact prior to tectonic movement. This is the first such zoogeographic connection reported for the family. The subfamily is not related to any Jamaican taxa tested. The Abbottellinae also do not occur on the southern Tiburon/Barahona peninsulas of Hispaniola, which has a different geologic history from the north. The eastern Cuban and Bahamian genus *Opisthosiphon* sensu lato was also shown to be a member of the subfamily. The nominal genus *Abbottella* is further divided into new genera based on these results. The new genera *Abbottipoma, Arenabbottella, Microabbottella,* and *Preclaripoma* are described. The new species *Rolleia simonaikeni* is described, and *Petasipoma* is synonomized with *Rolleia.*

Additional Keywords: Zoogeography, phylogenetics, Cuba, Hispaniola, new taxa, terrestrial gastropods, land snails

INTRODUCTION

The land snail family Annulariidae is an exclusively Caribbean/Central American group. For its limited geographic distribution it is extremely speciose with >700 recognized taxa (Watters, 2006). The major centers of diversity are Cuba, Hispaniola, and Jamaica. The snails are strict calciphiles and many species are highly endemic to a particular mountain range, mogote, or outcrop. Of these, the genus *Abbottella* was phylogenetically identified as a discrete clade apart from other annulariids by Skomrock (2014) and Watters and Larson (2017). Watters (2016b) formally raised the clade to subfamily level (Abbottellinae) based on additional radular and shell morphology characteristics. However, the questions of the origin of the subfamily and its relationships to other annulariids remained unanswered.

In all of the various schemes for higher annulariid systematics (Watters, 2006) subfamilies are distributed across the geographic range of the family – only the Abbottellinae, as previously understood, were endemic to a single portion of Hispaniola. Yet it may have been derived from elsewhere. In the Paleogene, proto-Central America was connected to Cuba and non-Tiburon Hispaniola, an association that may have lasted until the Eocene (Chakrabarty, 2006) or Miocene (Pindell, 1994) and provided ample time for faunal exchange. Since this time, these islands drifted east to their present positions, separating 20 to 25 million years ago (Pindell, 1994) and taking their snail faunas with them to further evolve in isolation. Buskirk (1985), reviewing the distributions of numerous groups of terrestrial animals (including snails) and pollen, also suggested a radiation from North and proto-Central America to the Greater Antilles by the Eocene. This would suggest a possible origin or connection for the abbottellines in Cuba or Jamaica.

This study examines the Abbottellinae based on phylogenetic, radular, and shell morphological considerations. In particular, membership to the subfamily is sought outside of Hispaniola in an attempt to determine: 1) if the group is indeed endemic to Hispaniola; 2) where might the origin of the group reside; and 3) what is its relation to the other subfamilies. Potential candidates are drawn from Cuba, Jamaica, and elsewhere based on similarities in shell morphology and radulae. Of particular interest are the similar-appearing *Annularia* of Jamaica and *Annularisca* of Cuba. In addition, the relationships between the recognized abbottelline genera are also examined.

Abbreviations used in the text are: ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BMSM,

[1] *In absentia*

Bailey-Matthews National Shell Museum, Sanibel, Florida, USA; GTW, collection of the author, Columbus, Ohio, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; OSUM, Ohio State University Museum of Biological Diversity, Columbus, Ohio, USA; UF, Florida Museum of Natural History, Gainesville, Florida, USA; USNM, National Museum of Natural History, Washington, DC, USA; ZMB, Zoologisches Museum Berlin, Federal Republic of Germany. Numbers in ( ) after catalog numbers refer to the number of specimens.

MATERIALS AND METHODS

To evaluate the phylogenetic placement of the Abbottellinae and to understand relationships among genera within Abbottellinae, we collected molecular sequence data from 19 individuals from Abbottellinae and 28 individuals from Annulariidae and Pomatiidae (Appendix1). We also downloaded data from 53 individuals from GenBank (NCBI nucleotide database) (Appendix1). As outgroups, we used *Pomatias elegans* (Müller, 1774) and *Tudorella ferruginea* (Lamarck, 1822) from Pomatiidae, and, as a more distant outgroup, *Littorina littorea* (Linnaeus, 1758) from Littorinidae. Samples collected for this study were stored in ethanol after collection, and DNA was extracted from foot tissues of preserved specimens using Qiagen DNeasy Blood and Tissue Kits (Qiagen Hiden, Germany) following the manufacturers standard protocol. A region of the mitochondrial gene 12S was sequenced using primers developed by Watters and Larson (2017). A region of cytochrome oxidase 1 (COI) was sequenced using universal invertebrate primers LCOI490 and HCO2198 (Folmer et al. 1994). The nuclear gene histone 3 (H3) was amplified using primers H3aF and H3aR (Colgan et al., 1998). PCR products were cleaned using ExoSAP-IT (Thremofisher Scientific) and sent to the Ohio State University Biomedical Research Tower for sequencing. Chromatograms were assembled in Geneious v6.1.7 (Kearse et al., 2012) and edited by eye when necessary. Sequences were aligned using the MUSCLE (Edgar, 2004) algorithm implemented in Geneious (Kearse et al., 2012) using default parameters.

The best model of nucleotide substitution and partitioning scheme was determined using PartitionFinder v2.1.1 (Lanfear et al., 2016). We used a greedy search scheme, considered all models of nucleotide substitution, and performed model selection using corrected AIC. A maximum-likelihood tree was inferred for COI using RAxML v8.2.10 (Stamatakis, 2014) as implemented on the Cipres Science Gateway (Miller et al., 2015). We used the partitioning scheme determined by PartitionFinder and the GTR model with Gamma rate variation. We used 100 bootstrap replicates to assess confidence in the inferred relationships. To infer a posterior distribution of gene trees, we used Bayesian Inference in MrBayes v3.2.2 (Ronquist et al., 2012). We used the partitioning scheme and models determined by PartitionFinder. Two independent analyses were run for 5,000,000 generations over four chains, sampling every 1,000 generations. We discarded 25% of runs as burn-in, and we assessed convergence using Tracer v1.6.0 (Rambaut and Drummond, 2007).

To infer a more robust hypothesis of relationships between groups, we used a concatenated dataset including the mitochondrial COI and 12S genes and the nuclear gene H3. While this dataset included fewer taxa than the COI dataset, it included a larger data matrix. Given that many taxa within Abbottellinae and those grouping with Abbottellinae in the COI gene tree could be included in this dataset and that relationships between these groups were not well resolved using COI (see Results), we analyzed this dataset in an attempt to further resolve relationships between these groups. While we acknowledge that a coalescent-based analysis would have been ideal (Edwards et al., 2016), given the limited sampling (2 independent loci, not sampled in all specimens), only a concatenation approach was possible for this study. All samples for which at least two of the three genes were sequenced were retained for this analysis. As above, we used PartitionFinder to select the best model and partitioning scheme, RAxML to infer a maximum likelihood tree, and MrBayes to infer the posterior distribution of trees under Bayesian inference.

Descriptions and measurements were based on shells oriented with the spire up and the aperture facing the viewer. Measurements are for adult shells unless noted otherwise. Length was measured from the tip of the protoconch (or teleoconch of decollate specimens) to the opposite anterior-most extension of the outer lip. Subsets of the largest and smallest adult specimens were selected by eye from all available specimens and measured to determine the minimum and maximum lengths. The number of whorls was determined using the 1 D method of Van Osselaer (1999).

Detailed redescriptions, accounts, and translated original descriptions of species previously covered can be found in Watters (2013, 2016b) and are not duplicated here. Distribution maps are Google™ Earth Pro. Image Landsat. © 2019 DigitalGlobe. Data: SIO, NOAA, US Navy, NGA, GEBCO.

RESULTS

Our final COI alignment included 82 individuals and 582 base pairs. The concatenated alignment of COI, 12S, and H3 included 50 individuals and 1,351 base pairs. For COI, the best scheme determined using AIC in PartitionFinder included three partitions (first, second, and third codon positions). The best models of nucleotide substitution were TVM+G, TRN+I+G, and GTR+I for the first, second, and third codon positions, respectively. The best scheme identified by

PartitionFinder for the concatenated dataset included seven partitions: One for each codon position of COI and H3 (for a total of six) and a single partitioning scheme for 12S. The best models inferred by PartitionFinder were TRN, JC+I, K81UF+G, GTR+G, HKY+G, TRN+G, and GTR+I for the first, second, and third codon positions of H3, 12S, and the first, second, and third codon positions of COI, respectively.

Abbottellinae was recovered as a monophyletic group (BS = 100, pp = 1.0) under both maximum likelihood and Bayesian inference of the COI gene tree (Figure 1), but there was not strong support for the relationship of this

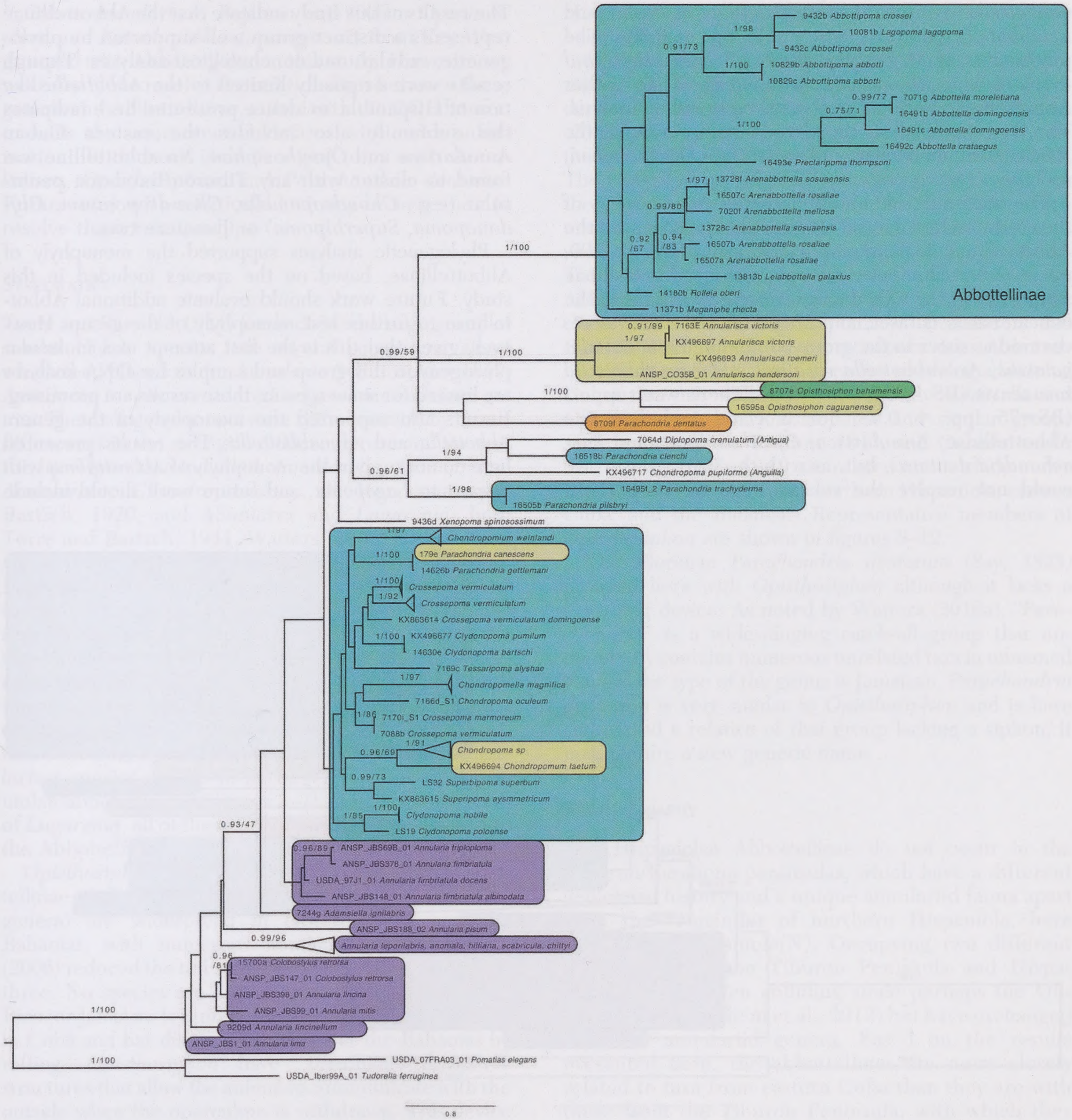


Figure 1. Maximum Likelihood tree based on COI. The numbers above the branches are posterior probability/ bootstrap support values. Support values are only shown for branches with either > 70 bootstrap support or >0.90 posterior probabilities. Taxa from the DR are highlighted in blue, taxa from Cuba are highlighted in yellow, taxa from the Bahamas are highlighted in green, taxa from Florida are highlighted in orange, and taxa from Jamaica are highlighted in purple. The Abbottellinae are labelled.

group to other sampled individuals. Within Abbottellinae, there were three moderately-to-well supported groups. One included *Abbottella moreletiana*, *Abbottella crataegus*, and *Abbottella domingoensis* (BS= 100, pp = 1.0). A moderately supported group (BS=73, pp = 0.91) included *Abbottipoma abbotti*, *Abbottipoma crossei*, and *Lagopoma lagopoma*. The third group included *Arenabbottella sosuaensis*, *Arenabbottella rosaliae*, *Arenabbottella mellosa*, and *Leiabbotella galaxius* (BS = 67, pp = 0.92). The placements of *Meganiphe rhecta*, *Rolleia oberi*, and *Preclaripoma thompsoni* with respect to other Abbottellinae were not well resolved in either analysis. The Bayesian analysis supported a group including the Hispaniolan abbottellines, *Annularisca*, *Opisthosiphon*, and *Parachondria dentatus* (BS = 59, pp = 0.99).

The maximum likelihood and Bayesian analyses of the concatenated dataset (Figure 2) also recovered the Abbottellinae as a monophyletic group (BS = 100, pp = 1.0). The same groups within Abbottellinae supported by the COI dataset were recovered with the concatenated dataset, and *Meganiphe rhecta* was recovered as sister to the group containing *Leiabbottella galaxius*, *Arenabbottella rosaliae*, and *Arenabbottella sosuaensis* (BS = 94, pp = 1.0). There was support (BS=75, pp = 0.98) for a clade including the Abbottellinae, *Annularisca*, *Opisthosiphon*, and *Parachondria dentatus*, but, as with the COI dataset, we could not resolve the relationships between these groups. There was also moderate support (BS = 62, pp = 0.96) for the other *Parachondria* as sister to this clade.

DISCUSSION

Molecular Phylogenetics

The results of this study indicate that the Abbottellinae represents a distinct group well-supported by phylogenetic, radular, and conchological analyses. Though results were originally limited to the *Abbottella*-like taxa of Hispaniola, evidence presented here indicates this subfamily also includes the eastern Cuban *Annularisca* and *Opisthosiphon*. No abbottelline was found to cluster with any Tiburon/Barahona peninsular (e.g., *Chondropomella*, *Chondropomium*, *Clydonopoma*, *Superbipoma*) or Jamaican taxa.

Phylogenetic analyses supported the monophyly of Abbottellinae, based on the species included in this study. Future work should evaluate additional Abbottellinae to further test monophyly of the group. However, given that this is the first attempt at a molecular phylogeny in this group and samples for DNA analyses are limited for some species, these results are promising. Results also supported the monophyly of the genera *Abbottella* and *Arenabbottella*. The results presented here do not support the monophyly of *Abbottipoma* with respect to *Lagopoma*, and future work should include

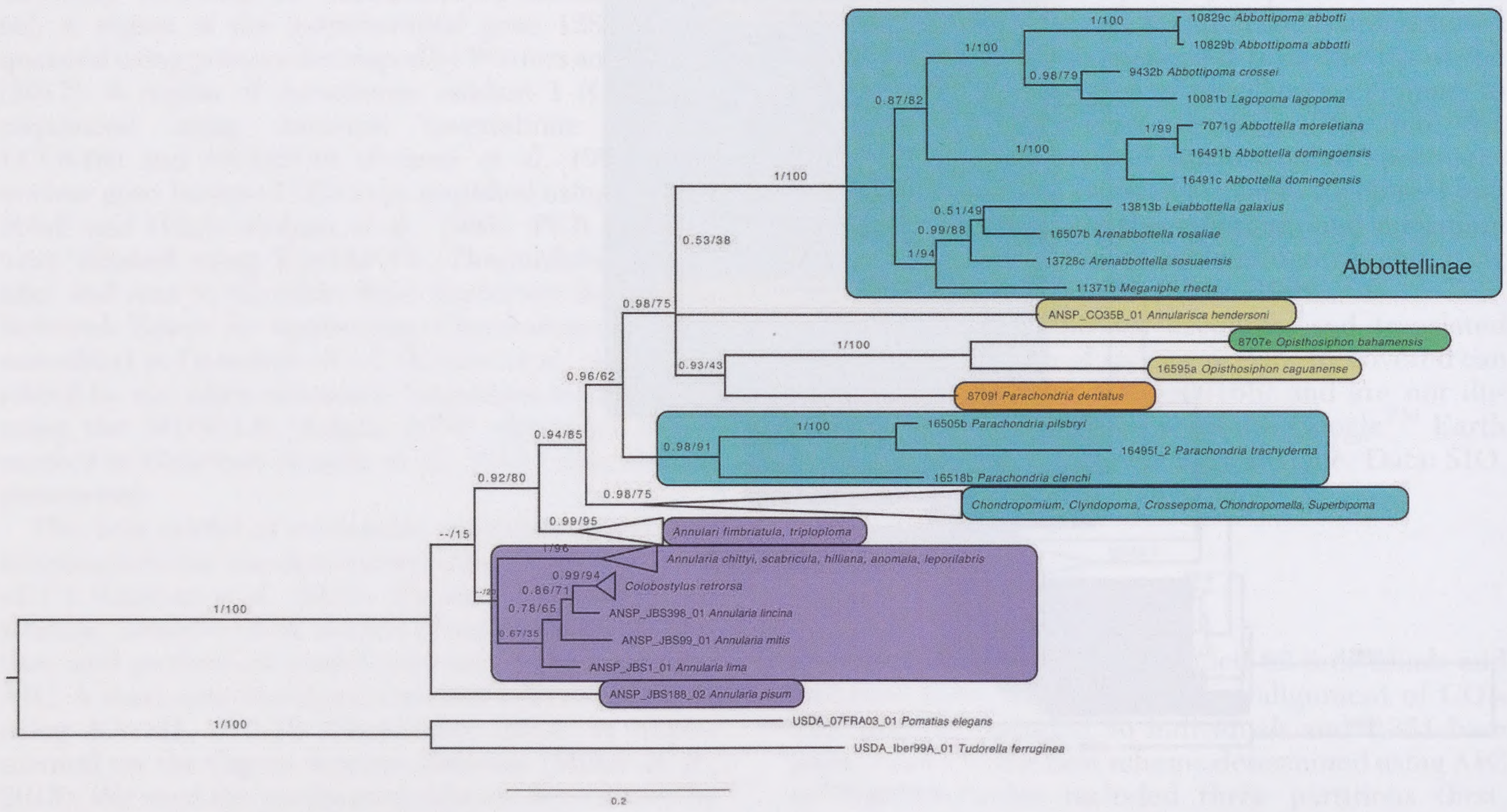


Figure 2. Maximum Likelihood tree based on the concatenated dataset. The numbers above the branches are posterior probability/bootstrap support values. Taxa from the DR are highlighted in blue, taxa from Cuba are highlighted in yellow, taxa from the Bahamas are highlighted in green, taxa from Florida are highlighted in orange, and taxa from Jamaica are highlighted in purple. The Abbottellinae are labelled.

additional representatives from *Lagopoma* to evaluate the monophyly of this group.

The Jamaican genera *Annularia* Schumacher, 1817, *Colobostylus* Crosse and Fischer, 1888, and *Adamsiella* Pfeiffer, 1851, were not found to be related to the Abbottellinae in this study. Although *Annularia* taxa have a similar shell form to abbottellines, the similarity is apparently due to convergence.

Cuban *Annularisca*, Bajaman and Cuban *Opisthosiphon*, and *Parachondria dominguensis* from Key West grouped with Abbottellinae in this study. However, we were unable to resolve the relationships between these groups and Abbottellinae, either with the COI dataset, or with the concatenated dataset with more information. Both trees include a polytomy with *Annularisca*, *Opisthosiphon*, and *Parachondria dentatus*. Future work with additional loci may be necessary to resolve these relationships.

Systematics

Torre and Bartsch (1941) finely divided a large group of similar Cuban species into several subgenera, all of which they placed under *Annularia* Schumacher, 1817. *Annularia* is now considered a Jamaican endemic genus. Their subgeneric taxa were differentiated by minor differences in the strength of the sculpture and form of the lip. These taxa included: *Annularella*, *Annularisca*, *Annularosa*, *Chondropomatus*, all Henderson and Bartsch, 1920, and *Annularex* and *Lugarenia*, both Torre and Bartsch, 1941. Watters (2006) consolidated all of these under the genus *Annularisca*, although *Lugarenia* is probably not related. They are all endemic to eastern Cuba. In addition to being phylogenetically sister to the Hispaniolan abbottellines, they share the same "Mitten" type radula (see below), similar opercular structure, and shell sculpture. *Annularisca* shell forms are very similar to *Abbottella* but consistently differ from those of other annulariids: low turbinoid, non-decollate, openly umbilicate shells. Cuban *Annularisca* species appear to be larger versions of Hispaniolan abbottellines (Figures 3–7). With the exception of *Lugarenia*, all of these Cuban taxa are here moved to the Abbottellinae.

Opisthosiphon was found to be part of the Abbottellinae clade as well. This genus (and its various subgenera) are widespread in eastern Cuba and the Bahamas, with numerous nominal species. Watters (2006) reduced the ten subgenera of previous workers to three. No species are known from Hispaniola, Puerto Rico, or Jamaica. It is probable that the genus originated in Cuba and has dispersed throughout the Bahamas by rafting. *Opisthosiphon* have "breathing" devices—structures that allow the animal to communicate with the outside when the operculum is withdrawn. This device varies from a simple pore to (more often) a short reflected siphon or snorkel. However, *Opisthosiphon* shares the "Mitten" type radula with abbottellines. It differs from the rest of the abbottellines in the following ways: the rhytidopomine operculum (pin-wheel extensions across the operculum rather than the single spiral lamellum of other abbottellines); the shells are decollated in *Opisthosiphon* but entire in the remainder of other abbottellines; the shell shape of *Opisthosiphon* is pupoid in overall shape rather than depressed turbinoid. Given the diversity of *Opisthosiphon* species in neighboring eastern Cuba, it is peculiar that none exist in Hispaniola. It is possible they did at one time but have been extirpated.

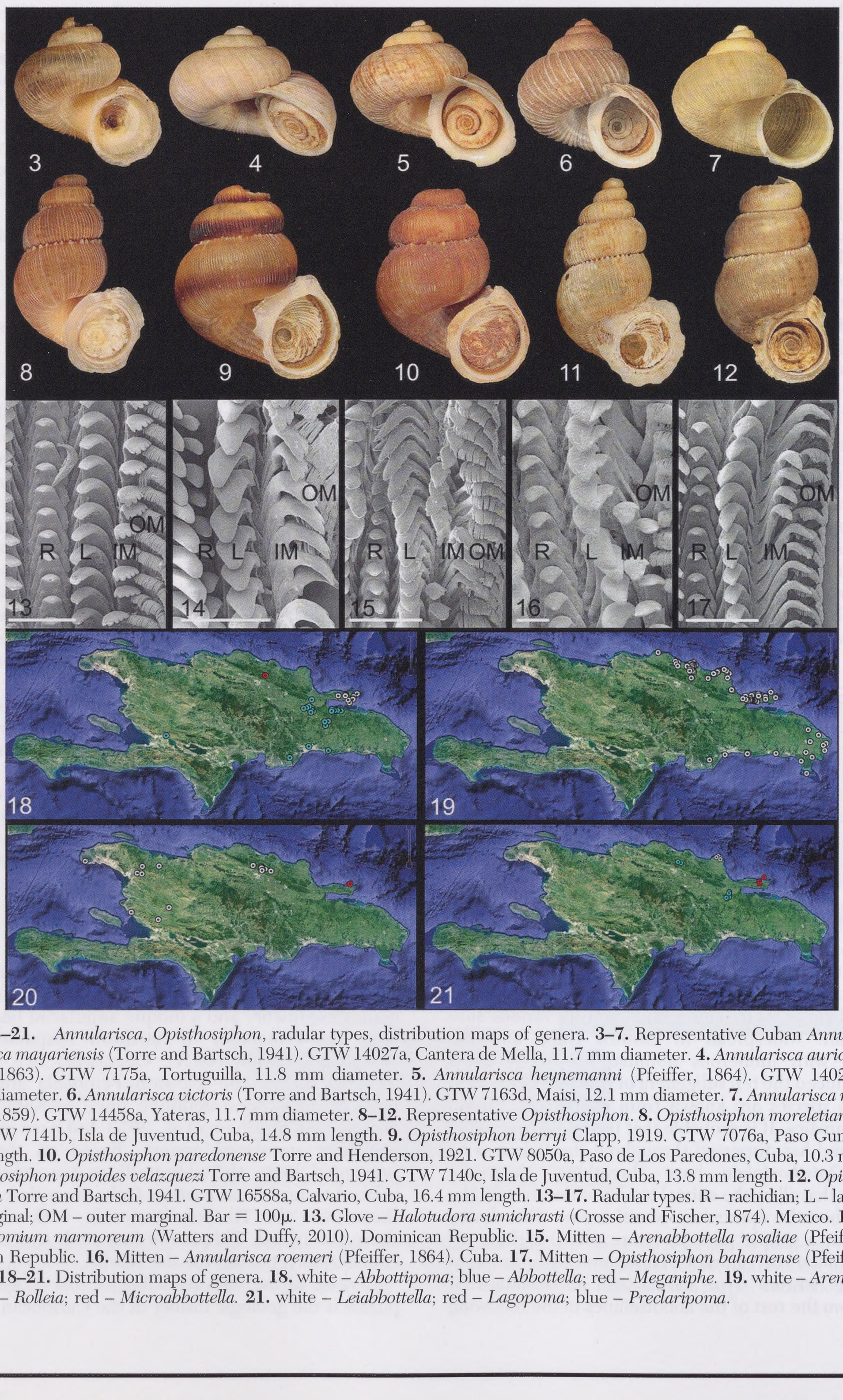
Opisthosiphon has been included in the Rhytidopominae, a heterogeneous group (as envisioned by Henderson and Bartsch, 1920) of Cuban taxa that Watters (2006) placed under the Chondropomatinae – a scheme that can no longer be maintained based on these results. The type genus is *Rhytidopoma* Sykes, 1901, based on the Cuban *Cyclostoma rugulosum* Pfeiffer, 1839, which resembles *Opisthosiphon* and has a breathing device as well. No *Rhytidopoma* taxa were available for this study. This presents a potential problem in the taxonomy of the Abbottellinae. If *Rhytidopoma* is part of the *Abbottella* clade, the nomen Rhytidopominae Henderson and Bartsch, 1920, would have precedence over Abbottellinae Watters, 2016. Future studies involving additional Cuban taxa may well show that not only *Abbottella* and *Opisthosiphon*, but *Rhytidopoma* and similar groups such as *Ramsdenia* Preston, 1913, and *Cubadamsiella* Torre and Bartsch, 1941, are related in one clade under Rhytidopominae that spans northern Hispaniola, eastern Cuba, and the Bahamas. Representative members of *Opisthosiphon* are shown in figures 8–12.

The Floridian *Parachondria dentatum* (Say, 1825) grouped here with *Opisthosiphon* although it lacks a breathing device. As noted by Watters (2016a), "*Parachondria*" is a wide-ranging catch-all group that undoubtedly contains numerous unrelated taxa in unnamed genera; the type of the genus is Jamaican. *Parachondria dentatum* is very similar to *Opisthosiphon* and is here considered a relative of that group lacking a siphon; it may require a new generic name.

Zoogeography

The Hispaniolan Abbottellinae do not occur in the Tiburon/Barahona peninsulas, which have a different geological history and a unique annulariid fauna apart from the remainder of northern Hispaniola, here designated Hispaniola(N). Occupying two different tectonic plates, the Tiburon Peninsula and Hispaniola(N) have been colliding since perhaps the Oligocene (van Benthem et al., 2013) but have exchanged very few annulariid genera. Based on the results presented here, the abbottellines are more closely related to taxa from eastern Cuba than they are with those from the Tiburon Peninsula, with which they share the island. This is the first such zoogeographic connection reported for the family.

Central to the understanding of this zoogeographic puzzle is the geologic history of the Caribbean. Eastern



Figures 3–21. *Annularisca*, *Opisthosiphon*, radular types, distribution maps of genera. **3–7.** Representative Cuban *Annularisca*. **3.** *Annularisca mayariensis* (Torre and Bartsch, 1941). GTW 14027a, Cantera de Mella, 11.7 mm diameter. **4.** *Annularisca auricoma putre* (Pfeiffer, 1863). GTW 7175a, Tortuguilla, 11.8 mm diameter. **5.** *Annularisca heynemanni* (Pfeiffer, 1864). GTW 14026a, Maisi, 14.2 mm diameter. **6.** *Annularisca victoris* (Torre and Bartsch, 1941). GTW 7163d, Maisi, 12.1 mm diameter. **7.** *Annularisca mackinlayi* (Pfeiffer, 1859). GTW 14458a, Yateras, 11.7 mm diameter. **8–12.** Representative *Opisthosiphon*. **8.** *Opisthosiphon moreletianum* (Petit, 1850). GTW 7141b, Isla de Juventud, Cuba, 14.8 mm length. **9.** *Opisthosiphon berryi* Clapp, 1919. GTW 7076a, Paso Gunaja, Cuba, 8.4 mm length. **10.** *Opisthosiphon paredonense* Torre and Henderson, 1921. GTW 8050a, Paso de Los Paredones, Cuba, 10.3 mm length. **11.** *Opisthosiphon pupoides velazquezi* Torre and Bartsch, 1941. GTW 7140c, Isla de Juventud, Cuba, 13.8 mm length. **12.** *Opisthosiphon cucullatum* Torre and Bartsch, 1941. GTW 16588a, Calvario, Cuba, 16.4 mm length. **13–17.** Radular types. R – rachidian; L – lateral; IM – inner marginal; OM – outer marginal. Bar = 100μ. **13.** Glove – *Halotudora sumichrasti* (Crosse and Fischer, 1874). Mexico. **14.** Hook – *Chondropomium marmoreum* (Watters and Duffy, 2010). Dominican Republic. **15.** Mitten – *Arenabbottella rosaliae* (Pfeiffer, 1858). Dominican Republic. **16.** Mitten – *Annularisca roemeri* (Pfeiffer, 1864). Cuba. **17.** Mitten – *Opisthosiphon bahamense* (Pfeiffer, 1865). Bahamas. **18–21.** Distribution maps of genera. **18.** white – *Abbottipoma*; blue – *Abbottella*; red – *Meganiphe*. **19.** white – *Arenabbottella*. **20.** white – *Rolleia*; red – *Microabbottella*. **21.** white – *Leiabbottella*; red – *Lagopoma*; blue – *Preclaripoma*.

Cuba and Hispaniola(N) were connected beginning with the Oligocene (Rosen, 1976; Judd, 2001; Ottenwalder, 2001), with Puerto Rico connected with eastern Hispaniola(N) from the middle Eocene to lower Miocene (Ottenwalder, 2001). When these were contiguous during the middle Cenozoic it formed an emergent pathway for dispersal from eastern Cuba (then a separate island from the remainder of Cuba) to the Cordillera Septentrional in northern Hispaniola and eastward to Puerto Rico. As a result, most of the terrestrial snail groups in Puerto Rico (van der Schalie, 1948) also occur in eastern Cuba. Most Hispaniolan abbottellines are endemic to the northern Cordillera Septentrional and its extension into the Samaná Peninsula. Similarly, the Cuban *Annularisca* inhabits the Sierra Maestra, the eastern mountain range, which is tectonically related to the Cordillera Septentrional and was an avenue for dispersal to Hispaniola(N)–but not to the Tiburon/Barahona peninsulas.

Cuba has been a "hot-spot" for annulariids with much of the diversity of this family apparently originating on that island. Containing nearly 300 of the approximately 700 recognized species, the Cuban taxa are some of the most diverse and probably encompass multiple unique lineages. The central location of the island, its complex geologic history of being at least three distinct islands, and evidence of being at least partially emergent since the middle Eocene (Graham, 2003) gives support to this island as a major center for annulariid origination and dispersal.

In Hispaniola the northern Cordillera Septentrional is separated from the Cordillera Central to the south by the Cibao Basin (Oligocene–Pliocene) (Edgar, 1991). The Cordillera Central is largely metamorphic and supports very few of these calciphilic snails. South of the Cordillera Central is the Sierra de Neiba, which although composed of limestone has no Abbottellinae. Clearly the granitic Cordillera Central acts as a barrier to dispersal from the northern Cordillera Septentrional to the southern Sierra de Neiba, and the Sierra de Neiba is the gateway to the Tiburon/Barahona peninsulas.

Some abbottelline groups are endemic to the Samaná Peninsula of eastern Hispaniola(N), which is of late-Miocene or early-Pliocene origin (inundated until Miocene (Joyce, 1991)). This modern day peninsula was an island even in historic times (Ross, 1921). Gabb (1873: 161) noted "the Gran Estero which separates Samaná from the main-land was a century ago a navigable channel, but is now entirely closed. It is said to have been closed by drift and mud from the [Río] Yuna." Cochran (1941: 2) commented: "Almost within the memory of the oldest inhabitant, Samaná Peninsula was an island separated from the main body of Hispaniola by a rapidly filling strait, in which pirate vessels were said to have lain in wait for richly laden merchantmen sailing for Europe." It is likely that some of the Abbottellinae evolved on that island rather than being invaders from the mainland and have never left (e.g., *Abbottipoma*, *Lagopoma*, *Microabbottella*).

SYSTEMATICS

Annulariidae Henderson and Bartsch, 1920

Type Genus: *Annularia* Schumacher, 1817.

Description: Shells to 42 mm in length, planispiral to high-spired, often with reflected lip at maturity. Spire typically decollate. Many taxa wholly or partially solute. Shell sculpture usually present, rarely produced into short spines or serrations. Spiral sculpture usually as cords or threads, axial sculpture as lamellae. In some Cuban and Bahamian taxa breathing devices are developed, varying from simple punctures to elaborate internal or external siphons. Operculum present, varying from paucispiral to multispiral. Operculum often with calcareous deposit that may take the form of erect spiral lamellae, overlapping plates, or pin-wheel-like extensions. Very few species with obvious periostracum consisting of bristle-like projections.

Animals with bifid snout and foot longitudinally bisected into lateral lobes. Locomotion ditaxic between lobes of foot. Snout produced into two short accessory tentacles that continuously sample substrate. Sexes separate.

Taenioglossate radula with rachidian, single pair of laterals, and two pairs of marginals. Rachidian and lateral teeth usually unicuspid, very rarely multicuspid. Inner marginal multicuspid. Outer marginal pectinate.

Remarks: The taenioglossate radula of annulariids is very conservative and only the inner marginal is of sufficient variability to be systematically informative. This tooth is categorized here as either a Glove, a Mitten, or a Hook based on its overall shape. The Glove type has a broad inner marginal tooth divided into blunt, shallowly indented cusps of varying strength and number (Figure 13). The Hook radula has a blunt, triangular tooth with weak cusps along the distal margin and a pronounced basal hook on the proximal side (Figure 14). The Mitten type has an elongated triangular tooth characterized by a single, small basal tooth on the distal side, rarely accompanied by weak serrations along the remainder of the distal margin (Figure 15). The Glove type is by far the most common radular type seen in >100 annulariid species examined (Watters, unpubl.). In contrast the Mitten type is the only radula found in the Abbottellinae (as here defined), including *Annularisca* (Figure 16) and *Opisthosiphon* (Figure 17). The Hook type is unique to a few genera (e.g., *Clydonopoma*) isolated on the Tiburon Peninsula of Hispaniola.

These snails spend an inordinate amount of time making more snails. Pairs are often found in a mating position even during dormant periods, with the male attached to the female on her right side. There appears to be a distinct sexual color dimorphism in some species (e.g., *Rolleia oberi*).

Many annulariids are highly endemic (Watters, 2017). The entire distribution of some species may consist of only a few kilometers (or less) of suitable habitat. Goodfriend and Mitterer (1988, 1993) found that

terrestrial snails in Jamaica have had relatively long spans of endemism, remaining in a single locality for thousands of years. They suggested that many terrestrial snails, at least in Jamaica, have persisted in place from the Late Pleistocene to the present (Goodfriend and Mitterer, 1988, 1993). Similarly, many of the main lineages within Annulariidae apparently have persisted for long periods of time and are the result of the separation and emergence of the major landmasses followed by the fragmentation of populations into discrete, isolated species.

Abbottellinae Watters, 2016

Description: Shells to 15 mm in diameter, pupoid to turbinoid to planispiral, with reflected lip at maturity. Spire decollate only in *Opisthosiphon* and relatives. Some taxa partially or completely solute. Shell sculpture usually present, varying from smooth to pustulose to short spines or serrations. Spiral sculpture, when present, of cords or threads, axial sculpture, when present, as lamellae. Operculum present, as multispiral, single, erect, calcareous plate or with pin-wheel ribs across surface in *Opisthosiphon* and relatives. Very few species with periostracum consisting of bristle-like projections. Radula taenioglossate, of Mitten type.

Remarks: In contrast to most annulariids, most abbottelline species normally have a nondecollated spire. But like other annulariids abbottellines may suspend themselves from mucus strands when at rest. This behavior has been found in numerous annulariid groups from many localities. It is not found in the sister group Pomatiidae and it must be a very ancient behavioral trait unique to the Annulariidae.

Key to Hispaniola Genera

1) Shell sculptureless or having only weak spiral cords in umbilicus 2
1) Shell not as above 3

2) Outer lip narrowly expanded ..... *Leiabbottella*
2) Outer lip widely expanded ..... *Preclaripoma*

3) Axial sculpture of widely spaced, prominent, erect, web-like lamellae ..... *Meganiphe*
3) Axial sculpture not as above 4

4) Sculpture spiny or serrated 5
4) Sculpture not as above 6

5) Shell nearly planispiral ..... *Abbottella*
5) Shell turbinoid ..... *Abbottipoma*

6) Outer lip notched *and* enrolled ..... *Lagopoma*
6) Outer lip not as above 7

7) Axial sculpture tightly packed, forming almost continuous layer, with prominent spiral keels ... . *Microabbottella*
7) Sculpture not as above 8

8) Spiral sculpture weaker than axial sculpture .... *Rolleia*
8) Spiral sculpture stronger than axial sculpture .... *Arenabbottella*

Genus *Abbottella* Henderson and Bartsch, 1920

Type Species: *Chondropoma moreletianum* Crosse, 1873, by original designation.

Description: Shell small (ca. 8–15 mm in diameter), depressed to planispiral, widely-umbilicate. Non-decollate. Widely expanded, often fimbriated or undulating outer lip, auriculate. Axial and spiral sculpture forming sharp cusps or serrations at their intersections. Multispiral operculum with erect or reflected, single calcified spiral lamella.

Distribution: Central Dominican Republic from the south coast to the Majugual area and the southern shore of Samaná Bay (but apparently absent from the Samaná Peninsula); only a single species has been found in Haiti (Figure 18).

Remarks: An undescribed species is known from a single specimen from San Pedro de Mecoris.

Etymology: William Louis Abbott (1860–1936), American physician, ornithologist, field naturalist, and patron of the United States National Museum, now National Museum of Natural History (USNM).

Key to Species

1) Sculpture of very fine spiral cords and axial lamellae, forming minute denticles, Haiti ..... haitensis
1) Sculpture coarse, forming denticles or thorny points, Dominican Republic 2

2) Final whorl with 40–80 axial lamellae, sculpture minutely serrated ..... domingoensis
2) Final whorl <50 axial lamellae, sculpture thorny 3

3) Final whorl with 30–40 axial lamellae, spiral opercular lamella reflected back over base ..... craetegus
3) Final whorl with 40–50 axial lamellae, spiral opercular lamella oblique but erect ..... moreletiana

***Abbottella crataegus* Watters, 2016**
(Figures 18, 22–28)

Chresonymy

Abbottella crataegus Watters, 2016: 116–117, figs. 17–24, 29.

Type Material: Holotype: UF 216138; Paratypes: UF 216138(5), from the type locality.

Type Locality: "5 km W of Majagual, Monte Plata Province, Dominican Republic."

Distribution and Habitat: Known only from the limestone outcrops near Majugual and Guaragao. This is the western part of the Cevicos Formation composed of karsted, massive limestone of upper Miocene–lower Pliocene age (Draper and Lewis, 1991). All specimens seen were found between 100–260 m elevation. Entire distribution may be <80 km^2. Snails live on mesic limestone outcrops.

Etymology: L. *crataegus*, a flowering thorny plant, a masculine noun in apposition.

Abbottella domingoensis Bartsch, 1946
(Figures 18, 29–36)

Chresonymy

Abbottella moreletiana gabriella Bartsch, 1946: 146, 148, pl. 25, figs. 4–6; Watters, 2006: 362.
Abbottella moreletiana wetmorei Bartsch, 1946: 146, 148, pl. 26, figs. 8–10.
Abbottella moreletiana domingoensis Bartsch, 1946: 147, pl. 25, figs. 1–3; Watters, 2006: 361–362.
Abbottella (*Abbottella*) *moreletiana domingoensis* (Crosse, 1873): Watters, 2006: 362.
Abbottella (*Abbottella*) *moreletiana gabriella* Bartsch, 1946: Watters, 2006: 83, 362; Watters, 2016b: 114–116 [in synonymy of *A. domingoensis*].
Abbottella (*Abbottella*) *moreletiana wetmorei* Bartsch, 1946: Watters, 2006: 83, 362.
Abbottella (*Abbottella*) *domingoensis* (Crosse, 1873): Watters, 2016b: 114–116, figs 9–16, 30.

Type Material: *Abbottella moreletiana domingoensis* Bartsch, 1946: Bartsch (1946) listed USNM 504118 as the holotype; this is now USNM 504117. *Abbottella moreletiana gabriella* Bartsch, 1946: Holotype: USNM 504124. *Abbottella moreletiana wetmorei* Bartsch, 1946: Holotype: USNM 504119.

Type Locality: *Abbottella moreletiana domingoensis* Bartsch, 1946: ""Santo Domingo," probably Santo Domingo City." *Abbottella moreletiana gabriella* Bartsch, 1946: "San Gabriel Isle, Samaná Bay." *Abbottella moreletiana wetmorei* Bartsch, 1946: "Pelican Keys, San Lorenzo Bay, Samaná Bay, Dominican Republic."

Distribution and Habitat: This species is found in the eastern end of the Cordillera Septentrional and the northern Cordillera Oriental in the Río Yuna valley and its tributaries; also in the low hills of the Los Ranchos Formation in the Sierra de El Seibo extending south to Santo Domingo and Boca Chica. It has been found under rocks and rubble on mesic limestone ridges where it is locally common. All specimens seen were found below 320 m elevation.

Remarks: *Abbottella moreletiana gabriella* Bartsch, 1946, is known only from San Gabriel Isle, just east of Boca del Infierno, possibly from the San Gabriel Cave (Angel Cave). *Abbottella moreletiana wetmorei* Bartsch, 1946, is known from the Pelican Keys. Both are here regarded as stunted forms of *A. domingoensis*. The name *Abbottella domingoensis* Bartsch, 1946, is here chosen as the valid name despite the page precedence of these two forms.

Etymology: *Abbottella moreletiana domingoensis* Bartsch, 1946: from Santo Domingo. *Abbottella moreletiana gabriella* Bartsch, 1946: from San Gabriel Isle. *Abbottella moreletiana wetmorei* Bartsch, 1946: Frank Alexander Wetmore (1886–1978), American ornithologist at Smithsonian Institution.

Abbottella haitensis Bartsch, 1946
(Figures 18, 37–39)

Chresonymy

Abbottella haitensis Bartsch, 1946: 143, 145–146, pl. 24, figs. 10–12.
Abbottella (*Abbottella*) *haitensis* Bartsch, 1946: Watters, 2006: 83, 287–288.

Type Material: Holotype: USNM 504111.

Type Locality: "[Haiti] on the road to Grand Bois, 4 miles north of Thomazeau, at an elevation of 1,000 feet." We have not located this Grand-Bois.

Distribution and Habitat: Known only from the type locality without habitat information.

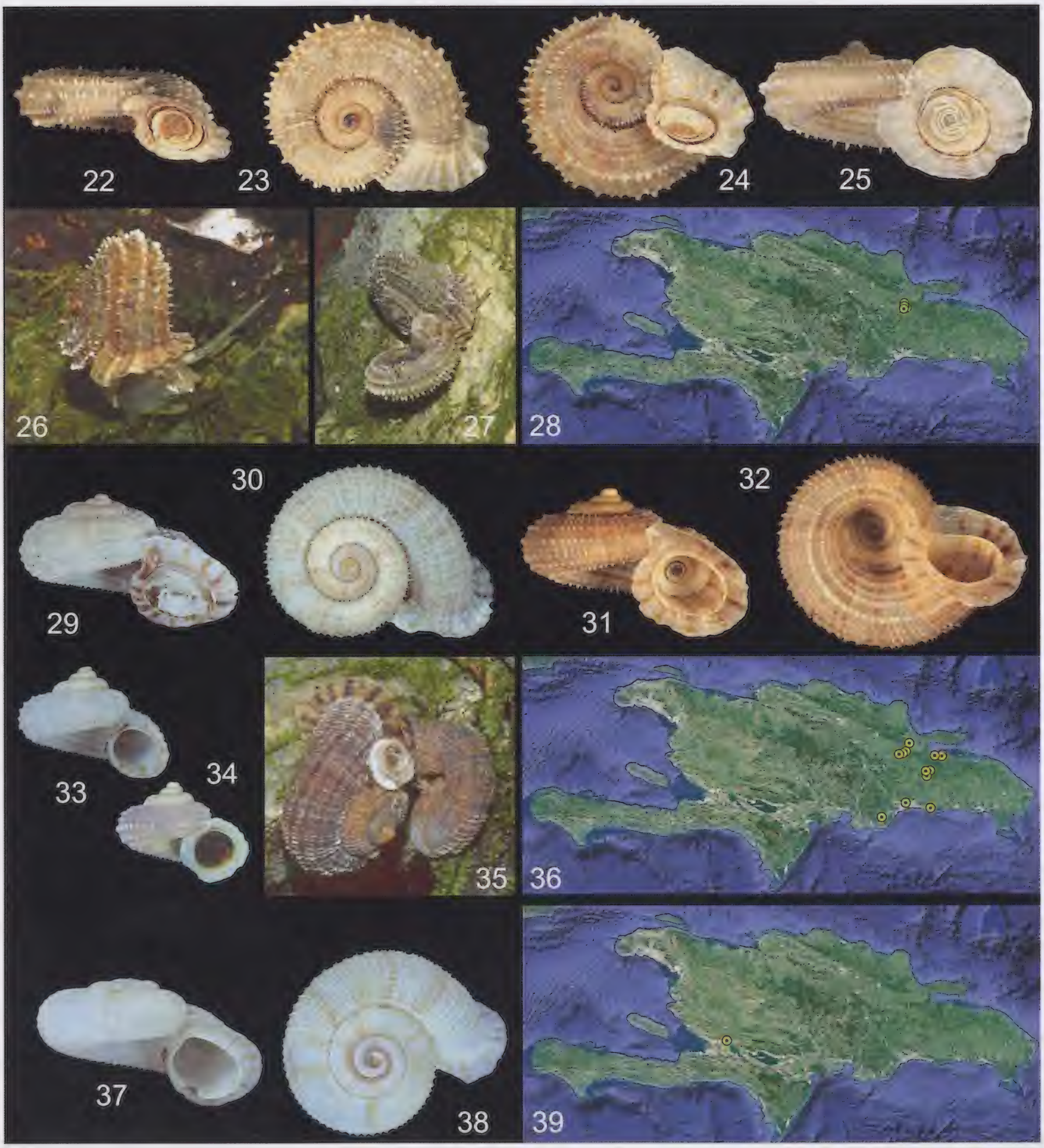
Remarks: This species is a mystery. It occurs so far from other *Abbottella* that it is tempting to believe it was mislocalized. However it was collected by the eminent field naturalist W.L. Abbott. The holotype label reads "1920" and Abbott was known to have collected in Haiti in 1920.

It is also possible this species belongs to a different genus. The pustulose sculpture is rather different from the spinose sculpture of the other *Abbottella*. The species also has some characteristics of *Rolleia*. Do not confuse with the similarly named *Rolleia haitensis* Bartsch, 1946.

Preserved material was not available.

Etymology: William Louis Abbott (1860–1936), American physician, ornithologist, field naturalist, and patron of the United States National Museum, now National Museum of Natural History (USNM).

Abbottella moreletiana moreletiana (Crosse, 1873)
(Figures 18, 40–43, 46)



Figures 22–39. *Abbottella*. **22–28.** *Abbottella crataegus* Watters, 2016. **22–24. Holotype**, UF 216138 (12.0 mm diameter). **25.** GTW 16492b (11.0 mm diameter). **26.** Live individual (photo S. Aiken ©). **27.** Mating pair (photo ©S. Aiken). **28.** Distribution map. **29–36.** *Abbottella domingoensis* Bartsch, 1946. **29, 30.** *Abbottella moreletiana domingoensis* Bartsch, 1946. **Holotype**, USNM 504117 (12.2 mm diameter). **31, 32.** UF 216133 (15.2 mm diameter). **33.** *Abbottella moreletiana gabriella* Bartsch, 1946: **Holotype**, USNM 504124 (8.6 mm diameter). **34.** *Abbottella moreletiana wetmorei* Bartsch, 1946: **Holotype**, USNM 504119 (7.0 mm diameter). **35.** Mating pair (photo S. Aiken ©). **36.** Distribution map. **37–39.** *Abbottella haitensis* Bartsch, 1946. **37, 38. Holotype**, USNM 504111 (12.7 mm diameter). **39.** Distribution map.

Chresonymy

Choanopoma moreletiana Crosse, 1873: 354; Crosse, 1874: 85, pl. 3, figs. 3, 3a; Pilsbry, 1933: 130; Watters, 2006:361.
Choanopoma moreletianum Crosse, 1873: Pfeiffer, 1876: 160–161; Kobelt, 1880: 277; Crosse, 1891: 168.
Tudorae [*sic*] *moreletianae* [*sic*] (Crosse, 1873): Arango, 1884: 211.
Abbottella moreletiana (Crosse, 1873): Henderson and Bartsch, 1920: 75; Thiele, 1931: 134; Abbott, 1989: 53; Watters, 2016b: 112, 114, figs. 1–8, 29.
Choanopoma (*Abbotella* [*sic*]) *moreletianum* Crosse, 1873: Clench and Aguayo, 1937: 67.
Chondropoma moreletianum (Crosse, 1874): Bartsch, 1946: 143.
Abbottella moreletiana moreletiana (Crosse, 1873): Bartsch, 1946: 147, pl. 25, figs. 10–12.
Abbottella (*Abbottella*) *moreletiana moreletiana* (Crosse, 1873): Watters, 2006: 361–362.

Type Material: Holotype: ANSP 14166, not figured in online database; from the Bland collection, collected by Gabb.

Type Locality: "*In regione Dominicanum insulae Haïti, Antillarum.*" Restricted by Watters (2016b) to "Sabana de la Mar, Hato Major Province, Dominican Republic."

Distribution and Habitat: It occurs on the southern side of Samaná Bay, including the nearshore Lower and Upper Orange keys, from approximately Boca del Infierno to Sabana de la Mar in Samaná and Hato Major provinces in the Los Haitises Limestone. This corresponds to the eastern part of the Cevicos Formation, composed of karsted, massive limestone blocks of Upper Miocene–Lower Pliocene age (Lebron and Mann, 1991). It is found in mesic forests in association with wet limestone cliffs, where it may be locally abundant. Its range may be <100 km^2.

Etymology: Named after Pierre Marie Arthur Morelet (1809–1892), French naturalist and conchologist working in Central America, Africa, and Europe.

Abbottella moreletiana kriegeri Bartsch, 1946
(Figures 44–46)

Chresonymy

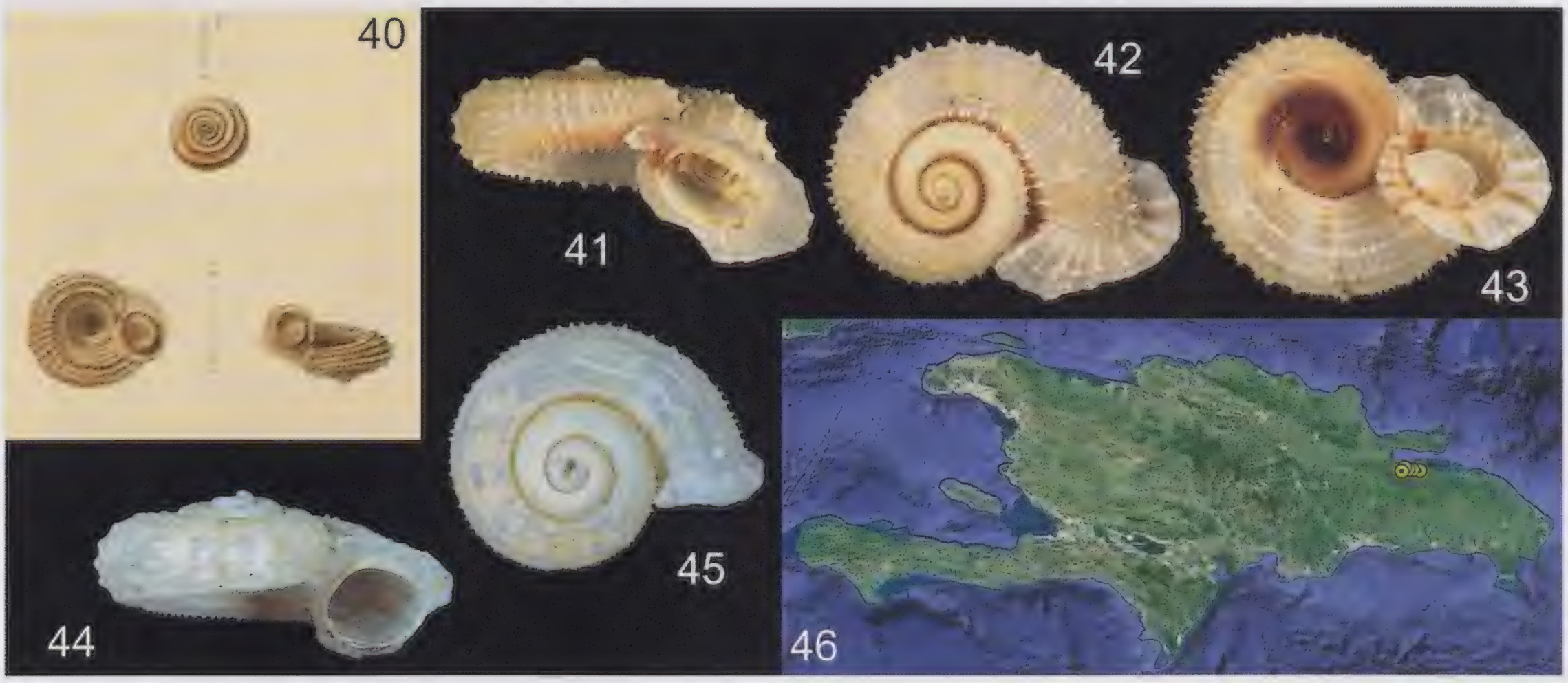
Abbottella moreletiana kriegeri Bartsch, 1946: 146, pl. 24, figs. 4–6.
Abbottella (*Abbottella*) *moreletiana kriegeri* Bartsch, 1946: Watters, 2006: 83, 362; Watters, 2016b: 112.

Type Material: Holotype: USNM 504115.

Type Locality: "North side of the Samaná Peninsula on the center of the south side of San Juan Bay, Dominican Republic." Based on Gabb's 1873 description and map, this apparently is the bay at Playa de Limón north of El Limón. However, *Abbottella* is not known from the Samaná Peninsula and this locality remains suspicious.

Distribution and Habitat: Known only from the possibly erroneus type locality without habitat infromation.

Remarks: We suspect this is a stunted form of *A. moreletiana* and the actual provenance is the south side of



Figures 40–46. *Abbottella*. **40–43.** *Abbottella moreletiana moreletiana* (Crosse, 1873). **40.** *Choanopoma moreletiana* Crosse, 1873. Crosse, 1874: 85, pl. 3, figs. 3, 3a. **41–43.** UF 216190 (12.3 mm diameter). **44, 45.** *Abbottella moreletiana kriegeri* Bartsch, 1946. **Holotype**, USNM 504115 (10.0 mm diameter). **46.** Distribution map.

Samaná Bay. Further collections will be needed to verify this. Preserved material was not available.

Etymology: Herbert William Krieger (1889–1970), American anthropologist at the Smithsonian Institution, collector of the type.

Genus *Abbottipoma* new genus

Type Species: *Abbottella abbotti* Bartsch, 1946.

Description: Shell small (ca. 6–10 mm in diameter), turbinoid, with spiral keels and minutely serrated or spiny sculpture, outer lip expanded and/or fimbriated or enrolled. Operculum as in family.

Distribution: Endemic to the eastern half of the Samaná Peninsula in mesic areas with limestone outcrops (Figure 18).

Etymology: *Abbottella abbotti*, the type species + *-poma*, a standard suffix for many annulariids.

Key to Species

1) Sculpture of coarse spines, outer lip deeply fimbriated ..... *abbotti*
1) Sculpture of minute serrations, outer lip not deeply fimbriated .....

2) Anterior margin of outer lip enrolled ..... *gabbi*
2) Anterior margin of outer lip not enrolled .... *crossei*

Abbottipoma abbotti (Bartsch, 1946)

(Figures 18, 47–54)

Chresonymy

Abbottella abbotti Bartsch, 1946: 143, 154–155, pl. 27, figs. 10–12.
Abbottella (*Abbottella*) *abbotti* Bartsch, 1946: Watters, 2006: 83, Watters, 2013: 11, figs. 3 A–E, 7 F.

Type Material: Holotype: USNM 504108. The type is a worn specimen that does not show the characteristic spiny sculpture.

Type Locality: "Near Laguna, Samaná Bay" [? Punta Laguna Salada, probable error for Samaná *Peninsula*, see Watters, 2013].

Distribution and Habitat: This narrowly endemic species occurs in the Sierra de Samaná of the Cordillera Septentrional in the El Valle and the Las Galeras areas on the northeast coast of the peninsula. A record from Cayo Levantado (GTW 10829a) seems unlikely and needs confirmation. Snails live below 50 m elevation on and at the base of limestone walls in cool, shaded areas with abundant mosses and other vegetation. It may occur in <10 km^2. At El Valle it lives within a few hundred meters of the beach in association with *Lagopoma lagopoma*, *Helicina salleana* Pfeiffer, 1852, and the very large pleurodontid *Caracolus excellens* (Pfeiffer, 1853).

Remarks: This species has been observed suspending itself by a mucus thread(s) from limestone outcrops.

Etymology: William Louis Abbott (1860 –1936), American physician, ornithologist, field naturalist, and patron of the United States National Museum, now National Museum of Natural History (USNM).

Abbottipoma crossei (Pilsbry, 1933)

(Figures 18, 55–62)

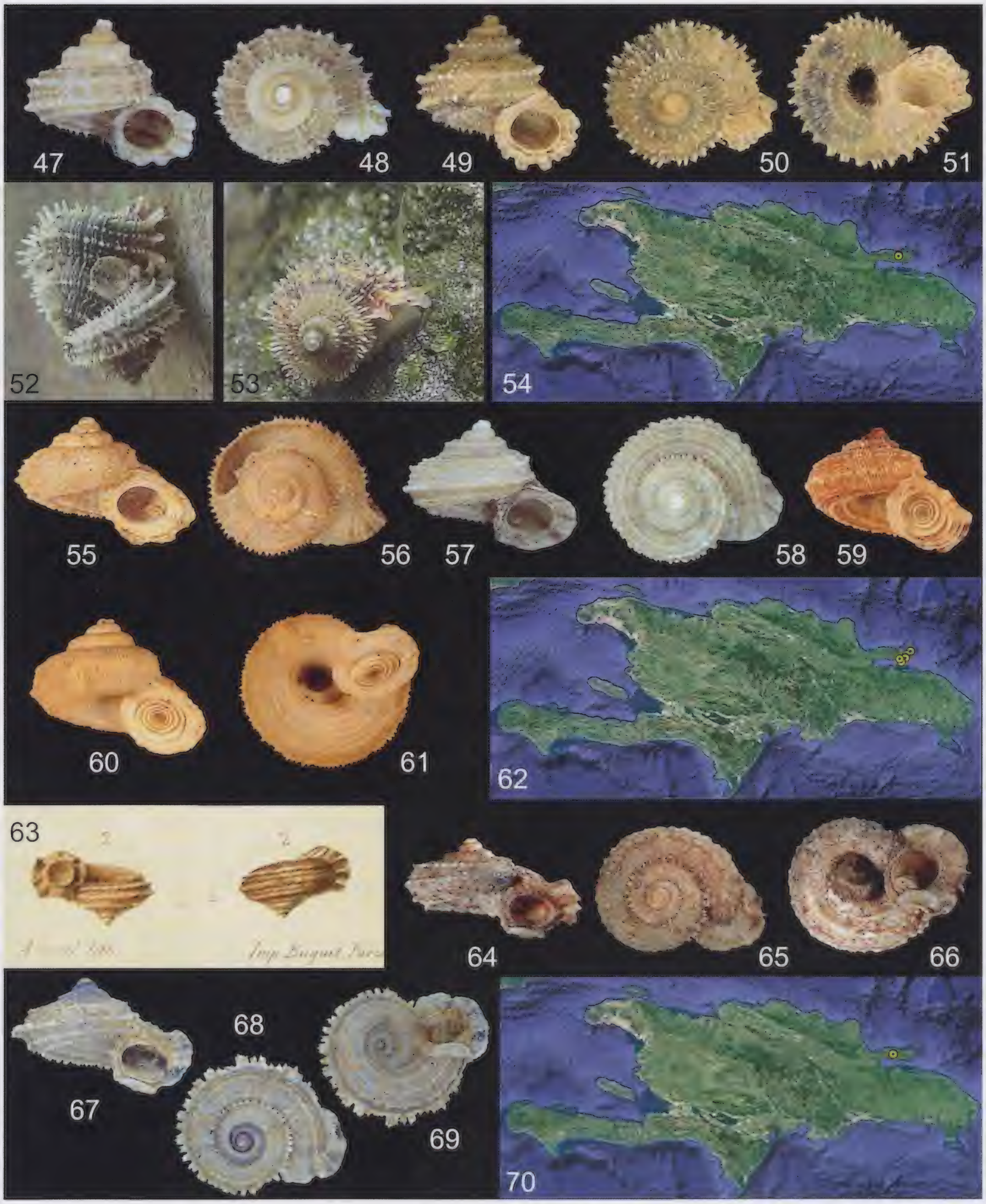
Chresonymy

Choanopoma crossei Pilsbry, 1933: 130, pl. 7, figs. 5, 5a, 6.
Abbottella crossei (Pilsbry, 1933): Bartsch, 1946: 144, 153, pl. 27, figs. 13–15.
Abbottella gabbi pilsbryi Bartsch, 1946: 152–153, pl. 27, figs. 7–9.
Rolleia crossei (Pilsbry, 1933): Baker, 1964: 169.
Abbottella (*Abbottella*) *crossei* (Pilsbry, 1933): Watters, 2006: 83, 222; Watters and Duffy, 2010a: 2; Watters, 2013: 14, figs. 3 S–W, 7 G.
Abbottella (*Abbottella*) *gabbi pilsbryi* Bartsch, 1946: Watters, 2006: 83, 269.
? *Abbottella* (*Abbottella*) *harpeza* Watters and Duffy, 2010a: 1–2, figs. 1–3.

Type Material: *Choanopoma crossei* Pilsbry, 1933: Holotype: ANSP 7951; Paratype: ANSP 373769(1). The type lot of *A. gabbi* contained two species, *gabbi* and *crossei*. Pilsbry (1933) designated Crosse's figured specimen of the lot as the type of *A. gabbi*. *Abbottella gabbi pilsbryi* Bartsch, 1946: Holotype: USNM 504099. *Abbottella harpeza* Watters and Duffy, 2010: Holotype: UF 420731.

Type Locality: *Choanopoma crossei* Pilsbry, 1933: "Santo Domingo." Restricted by Watters (2013) to "4 km E of Samaná, Samaná Province, Dominican Republic." *Abbottella gabbi pilsbryi* Bartsch, 1946: "in a cave on the Río Seco near Samaná, Samaná Bay, Dominican Republic." *Abbottella harpeza* Watters and Duffy, 2010: "Isla Beata," probably in error for Samaná Peninsula.

Distribution and Habitat: This species inhabits the coastal limestone bluffs of the eastern Samaná Peninsula in the Sierra de Samaná including Cayo Levantado. Specimens have been found on limestone outcrops in fields and on cliffs and stone walls, often abundant; occasionally arboreal. All specimens seen were found below 50 m elevation.



Figures 47–70. *Abbottipoma.* **47–54.** *Abbottipoma abbotti* (Bartsch, 1946). **47, 48. Holotype**, USNM 504108 (6.0 mm diameter). **49–51.** GTW 10829b (7.1 mm diameter). **52.** Mating pair. **53.** Live individual. **54.** Distribution map. **55–62.** *Abbottipoma crossei* (Pilsbry, 1933). **55, 56.** *Choanopoma crossei* Pilsbry, 1933. **Holotype**, ANSP 7951 (7.5 mm diameter, photo courtesy of ANSP). **57, 58.** *Abbottella gabbi pilsbryi* Bartsch, 1946. **Holotype**, USNM 504099 (7.5 mm diameter). **59.** *Abbottella* (*Abbottella*) *harpeza* Watters and Duffy, 2010. **Holotype**, UF 420731 (7.1 mm diameter). **60, 61.** GTW 9432a (7.3 mm diameter). **62.** Distribution map. **63–70.** *Abbottipoma gabbi* (Crosse, 1873). **63.** *Choanopoma gabbi* Crosse, 1873. Crosse, 1874: 84, pl. 3, fig. 2. **64–66. Syntype**, MNHN 2000-5452 (7.4 mm diameter, photo courtesy of Manuel Caballer, MNHN). **67–69.** Julian Joseph coll. (6.3 mm diameter, photos ©S. Aiken). **70.** Distribution map.

Remarks: *Abbottella harpeza* Watters and Duffy, 2010, was described from Isla Beata. This now seems very unlikely, being far out of the range of all other abbottellines, and probably represents a mislocalized specimen. Additional study at Isla Beata is needed to confirm this.

Etymology: *Choanopoma crossei* Pilsbry, 1933: Joseph Charles Hippolyte Crosse (1826–1898), French conchologist, editor of the *Journal de Conchyliologie*. *Abbottella gabbi pilsbryi* Bartsch, 1946: Henry Augustus Pilsbry (1862–1957), American conchologist, Academy of Natural Sciences of Philadelphia. *Abbottella harpeza* Watters and Duffy, 2010: L. *harpeza*, a thorny bush, a thicket.

Abbottipoma gabbi (Crosse, 1873)

(Figures 18, 63–70)

CHRESONYMY

Choanopoma gabbi Crosse, 1873: 353–354; Crosse, 1874: 84, pl. 3, fig. 2; Pfeiffer, 1876: 159; Kobelt, 1880: 277; Crosse, 1891: 168; Henderson and Bartsch, 1920: 75; Pilsbry, 1933: 129–130, pl. 7, figs. 1–4; Fischer-Piette, 1950: 80.

Abbottella gabbi (Crosse, 1873): Henderson and Bartsch, 1920: 75.

Abbottella gabbi gabbi (Crosse, 1873): Bartsch, 1946: 144, 152, pl. 26, figs. 5–7.

Abbottella (*Abbottella*) *gabbi gabbi* (Crosse, 1873): Watters, 2006: 83, 269.

Type Material: Syntype: MNHN 2000-5452 (Only one specimen mentioned in database, number of additional specimens unknown). This specimen is a worn example.

Type Locality: "*in regione Dominicanum insulae Haïti, Antillarum.*" Restricted here to "near El Salto del Limón, central Samaná Peninsula, Samaná Province, Dominican Republic."

Distribution and Habitat: This unlocalized species was recently rediscovered after nearly 150 years at El Salto del Limón in the central Samaná Peninsula. It was found in "soil/leaf litter around coral/limestone boulders along the edge of the forest path" to the waterfall (J. Joseph, 2017, pers. comm.).

Remarks: The combination of the enrolled anterior portion of the outer lip, purple apex, and strong, spiral, fimbriated carinations is unique. Preserved material was not available.

Etymology: William More Gabb (1839–1878), American geologist and paleontologist who surveyed in Hispaniola.

Genus Arenabbottella new genus

Type Species: *Abbottella sosuaensis* Bartsch, 1946.

Description: Shells small (6–11 mm in diameter), turbinoid, sculpture of minute pustules or weak serrations on more-or-less well-developed spiral cords often forming weak keels, cords often prominent in umbilicus, suture channeled, outer lip expanded, often auriculate. Lip may be folded or rolled abaperturely to varying degrees. Sculpture is often arranged in axial "blocks" probably representing growth lines.

Distribution: This is the most widely distributed abbottelline group, occurring around the eastern half of the island on the northern slopes of the Cordillera Septentrional from Luperon to the Samaná Peninsula and around the southeastern lowlands from Las Lagunas de Nisibon to San Cristobal, including Isla Saona (Figure 19). Snails live under leaf litter and limestone rubble, from open fields to mesic forests.

Remarks: This is the most speciose of the Hispaniolan abbottelline genera. Based on conchological features and distributional patterns, there seems to be a split below Samaná Bay between a northern and a southern group of species but none of the northern species were available for phylogenetic study. These two groups may yet be found to constitute different genera.

Etymology: L. *arenosus*, full of sand + *Abbottella*; in reference to the sandy sculpture of the shells.

Key to Species

The questionable taxa *Choanopoma adolfi* Pfeiffer, 1852, and *Cyclostoma tentorium* Pfeiffer, 1850, are not included.

1) Columellar side of outer lip enrolled ... *samanaensis*
1) Columellar side of outer lip not enrolled 2

2) Outer lip fimbriated ..... *rosaliae*
2) Outer lip not fimbriated 3

3) Shell with a prominent central, serrated keel ..... *calliotropis*
3) Shell without a prominent keel 4

4) Outer lip narrowly expanded 5
4) Outer lip widely expanded 8

5) Sculpture nearly obsolete, shell with a metallic sheen ..... *nitens*
5) Sculpture not as above 6

6) Final whorl with ca. 120 axial lamellae, shell usually white ..... *milleacantha*
6) Final whorl with <100 axial lamellae, shell usually copper-colored 7

7) Final whorl with ca. 90 axial lamellae, eastern .... *aenea*
7) Final whorl with ca. 70 axial lamellae, western .... *urbana*

8) Sculpture nearly obsolete except for umbilicus, shells rather smooth 9
8) Sculpture of minute but well-developed serrations 11

9) Strong spiral cords absent from umbilicus .... *tenebrosa*
9) Strong spiral cords present in umbilicus 10

10) Shell pale yellow with brown spots, suture with white, random denticles ..... *mellosa*
10) Shell brown without spots, suture lacking white, random denticles ..... *newcombi*

11) Strong spiral cords absent from umbilicus 12
11) Strong spiral cords present in umbilicus 13

12) Shell pale brown or yellow, sculpture fine .... *wilhelmi*
12) Shell dark brown or white, sculpture coarse .... *dichroa*

13) Spiral cords not all of uniform strength, outer lip widely expanded ..... *anchezi*
13) Spiral cords approximately the same strength, outer lip narrowly expanded ..... *sosuaensis*

***Arenabbottella adolfi* (Pfeiffer, 1852)**
(Figures 19, 71, 72)

CHRESONYMY

Choanopoma adolfi Pfeiffer, 1852a: 167; Pfeiffer, 1853: 117–118; Adams and Adams, 1856: 296; Hjalmarson and Pfeiffer, 1858: 139; Pfeiffer, 1858b: 102; Kobelt, 1880: 277; Crosse, 1891: 166.
Cyclostoma (*Choanopoma*) *adolfi* (Pfeiffer, 1852): Pfeiffer, 1854a: 142.
Cyclostoma adolfi (Pfeiffer, 1852): Pfeiffer, 1854c: pl. 48, figs. 5–8; Pfeiffer, 1854d: 371.
Choanopoma adolphi [*sic*] Pfeiffer, 1852: Bland, 1861: 355; Pfeiffer, 1865: 111; Pfeiffer, 1876: 161.
Cyclostoma adolphi [*sic*] (Pfeiffer, 1852): Reeve, 1862: pl. 22, fig. 146.
Abbottella adolphi [*sic*] (Pfeiffer, 1852): Henderson and Bartsch, 1920: 75.
Abbottella adolphi adolphi [*sic*] (Pfeiffer, 1852): Bartsch, 1946: 143, 149–150, pl. 26, fig. 4.
Abbottella (*Abbottella*) *adolfi adolfi* (Pfeiffer, 1852): Watters, 2006: 83, 130.
Abbottella adolfi (Pfeiffer, 1852): Watters and Duffy, 2010a: 2.
non Abbottella (*Abbottella*) cf. *adolfi adolfi* (Pfeiffer, 1852): Watters, 2013: 13, figs. 3 F–I, 9 D [= *A. mellosa*].

Type Material: The type has apparently been lost. Many of Pfeiffer's types were probably destroyed by Allied bombing of the Museum Naradone in Szczecin, Poland, in WW II.

Type Locality: *"Habitat in insula Haiti."*

Distribution and Habitat: Known only from the unlocalized type locality without habitat information.

Remarks: Pfeiffer (1854: pl. 48, figs. 5–8) and Reeve (1862: pl. 22, fig. 146) illustrated it but it cannot be confidently identified from these figures. It is here considered a *nomen dubium*.

Etymology: Probably Emil Adolf Rossmässler (1805?–1867), German conchologist.

***Arenabbottella aenea* (Watters, 2010)**
(Figures 19, 76–79)

CHRESONYMY

Abbottella (*Abbottella*) *aenea* Watters, 2010: 16–17, text fig., pl. 1, figs. 1–4; Watters, 2013: 13, figs. 3 N–R, 8 C.

Type Material: Holotype: UF 434777; Paratype: UF 434778(1); Paratypes: BMSM 17971(2); Paratypes: OSUM 35490(2), all from the type locality.

Type Locality: "Dominican Republic, La Altagracia Province, Punta Cana."

Distribution and Habitat: Known only from the type locality. Specimens were found under moldy leaf litter.

Remarks: Preserved material was not available.

Etymology: L. *aeneus*, copper.

***Arenabbottella calliotropis* (Watters, 2013)**
(Figures 19, 80–83)

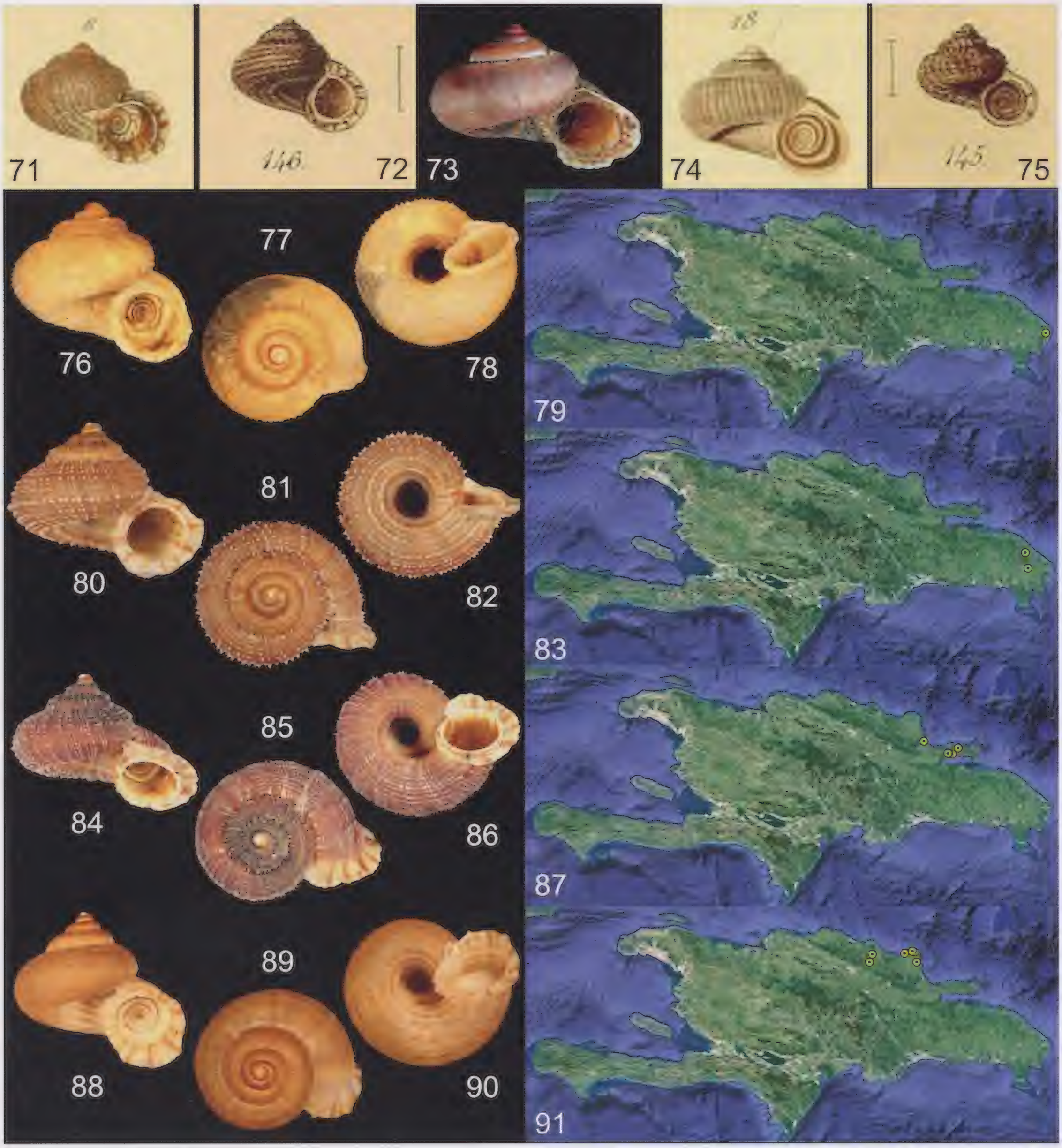
CHRESONYMY

Abbottella (*Abbottella*) *calliotropis* Watters, 2013: 3, figs. 1 A–E, 5 O, 7 A.

Type Material: Holotype: UF 456810; Paratypes: UF 216131(59), from the type locality.

Type Locality: "Dominican Republic, La Altagracia Province, along Río Yuna, 2 km S of La Guana. ca. 18.79° N, – 68.67° W."

Distribution and Habitat: Under limestone rubble in fields on the easternmost outcrops of the cordillera in La Altagracia Province in the area of Higüey and Las Lagunas de Nisibon.



Figures 71–91. *Arenabbottella*. **71, 72.** *Arenabbottella adolfi* (Pfeiffer, 1852). **71.** *Choanopoma adolfi* Pfeiffer, 1852. Pfeiffer, 1854c: pl. 48, fig. 8. **72.** *Cyclostoma adolphi* [*sic*] (Pfeiffer, 1852): Reeve, 1862: pl. 22, fig. 146. **73.** *Arenabbottella newcombi* (Crosse, 1873). **Syntype**, MNHN 5436 (photo courtesy of MNHN). **74, 75.** *Arenabbottella tentorium* (Pfeiffer, 1850). **74.** *Cyclostoma tentorium* Pfeiffer, 1850. Pfeiffer, 1854b: pl. 38, fig. 18. **75.** *Cyclostoma tentorium* Pfeiffer, 1850. Reeve, 1862: pl. 22, fig. 145. **76–79.** *Arenabbottella aenea* (Watters, 2010). **76–78.** GTW 14181a (6.5 mm diameter). **79.** Distribution map. **80–83.** *Arenabbottella calliotropis* (Watters, 2013). **80–82. Holotype**, UF 456810 (7.5 mm diameter). **83.** Distribution map. **84–87.** *Arenabbottella dichroa* (Watters, 2013). **84–86. Holotype**, UF 456801 (9.9 mm diameter). **87.** Distribution map. **88–91.** *Arenabbottella mellosa* (Watters and Duffy, 2010). **88–90.** GTW 7020c (5.0 mm diameter). **91.** Distribution map.

Remarks: Preserved material was not available.

Etymology: Gr. *kallos*, beauty + Gr. *trope*, a turning.

***Arenabbottella dichroa* (Watters, 2013)**
(Figures 19, 84–87)

CHRESONYMY

Abbottella (*Abbottella*) *dichroa* Watters, 2013: 6–7, figs. 1 K–O, 5 Q, 7 C.

Type Material: Holotype: UF 456801; Paratypes: UF 216112(31), from the type locality.

Type Locality: "Dominican Republic, Samaná Province, just E of El Limón, 10 km E of Las Terrenas, at sea level. ca. 19.29° N, –69.44° W."

Distribution and Habitat: Known from the north coast of the Sierra de Samaná of the Cordillera Septentrional from the western Samaná Peninsula to Nagua on limestone hills in mesic, shaded forests.

Remarks: This species is peculiar in having two color morphs in the same population: white or brown. This may be due to sexual dimorphism. Preserved material was not available.

Etymology: Gr. *di-*, two + Gr. *chroa*, color of the skin; in reference to the two color morphs.

***Arenabbottella mellosa* (Watters and Duffy, 2010)**
(Figures 19, 88–91)

CHRESONYMY

Abbottella (*Abbottella*) *mellosa* Watters and Duffy, 2010a: 2, figs. 4–6; Watters, 2013: 8, fig. 1 T.
Abbottella (*Abbottella*) cf. *adolfi adolfi* (Pfeiffer, 1852): Watters, 2013: 13, figs. 3 F–I, 9 D.

Type Material: Holotype: UF 420729; Paratype: OSUM 32477(1), from the type locality.

Type Locality: "Dominican Republic, Los Brazos, near Sosúa."

Distribution and Habitat: Known only from three adjacent outcrops: Loma Catalina and Loma Blanca near Sosúa and the outcrop near Río San Juan on the northern coast. All specimens seen were found below 70 m elevation.

Remarks: Rare, well-preserved specimens have periostracal hairs.

Etymology: L. *mellosa*, honey-colored.

***Arenabbottella milleacantha* (Watters and Duffy, 2010)**
(Figures 19, 92–95)

CHRESONYMY

Abbottella (*Abbottella*) *milleacantha* Watters and Duffy, 2010a: 2–3, figs. 7–9; Watters, 2013: 4, 7, 13, 14, figs. 3 X–BB, 7 H.

Type Material: Holotype: UF 420728; Paratype: OSUM 32478(1), from the type locality.

Type Locality: "Dominican Republic, northeast Isla Saona."

Distribution and Habitat: This species occurs on Isla Saona and the adjacent coast from San Pedro de Macoris to Bavaro in sub-mesic to mesic forests along limestone ridges under blocks and in leaf litter; also in caves.

Remarks: Preserved material was not available.

Etymology: L. *mille*, thousand + Gr. *akantha*, thorn, prickle.

***Arenabbottella newcombi* (Crosse, 1873)**
(Figure 73)

CHRESONYMY

Choanopoma newcombi Crosse, 1873: 352–353; Crosse, 1874: 82, pl. 3, figs. 1, 1a; Pfeiffer, 1876: 160; Kobelt, 1880: 277; Crosse, 1891: 167–168; Fischer-Piette, 1950: 79–80.
Abbottella newcombi (Crosse, 1873): Henderson and Bartsch, 1920: 75; Bartsch, 1946: 143, 144–145, pl. 24, figs. 7–9.
Abbottella (*Abbottella*) *newcombi* (Crosse, 1873): Watters, 2006: 83, 371; Watters, 2013: 13.

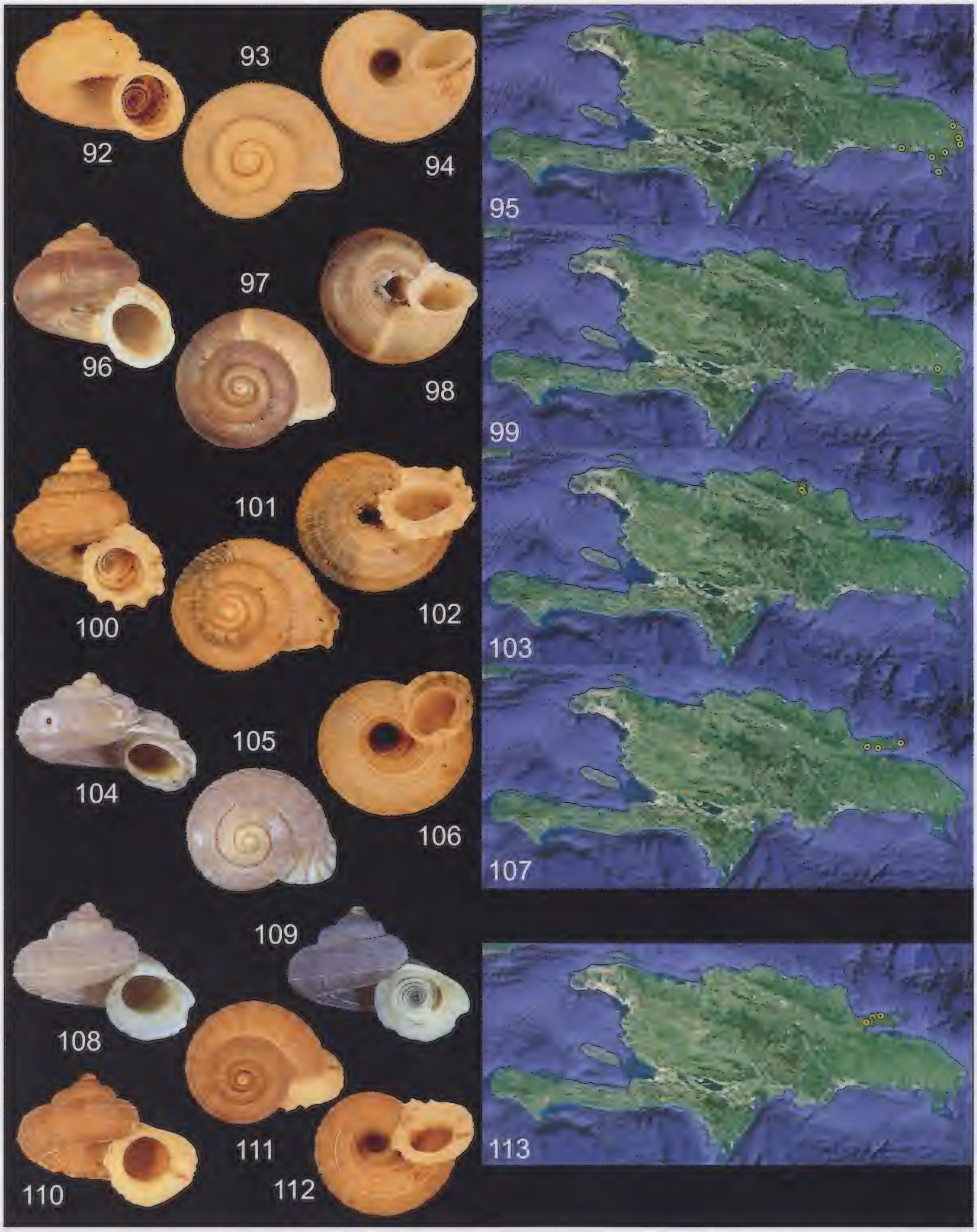
Type Material: Syntype: MNHN 5436.

Type Locality: *"in regione Dominicanum insulae Haïti, Antillarum."*

Distribution and Habitat: Known only from the unlocalized type locality.

Comparison with Other Species: Based on two specimens, this is a relatively smooth, brown shell with a deep suture and lacking keels.

Remarks: Bartsch's (1946) specimens were received from Newcomb but with only "Santo Domingo" as their provenance, undoubtedly referring to the country rather than the city. Although clearly a member of this group it has not been collected since its description.



Figures 92–113. *Arenabbottella*. **92–95.** *Arenabbottella milleacantha* (Watters and Duffy, 2010). **92–94. Holotype**, UF 420728 (7.5 mm diameter). **95.** Distribution map. **96–99.** *Arenabbottella nitens* (Watters, 2013). **96–98. Holotype**, UF 456806 (7.8 mm diameter). **99.** Distribution map. **100–103.** *Arenabbottella rosaliae* (Pfeiffer, 1858). **100–102.** UF 216191 (9.2 mm diameter). **103.** Distribution map. **104–107.** *Arenabbottella samanensis* (Bartsch, 1956). **104, 105. Holotype**, USNM 504090 (10.6 mm diameter). **106.** GTW 7085c (8.7 mm diameter). **107.** Distribution map. **108–113.** *Arenabbottella sanchezi* (Bartsch, 1946). **108.** *Abbottella sanchezi* Bartsch, 1946. **Holotype**, USNM 504092 (9.1 mm diameter). **109.** *Abbottella adolphi peninsularis* Bartsch, 1946. **Holotype**, USNM 504095 (9.8 mm diameter). **110–112.** UF 216154 (9.1 mm diameter). **113.** Distribution map.

Etymology: Wesley Newcomb (1808–1892), American physician, conchologist, Hawaiian temperance leader.

***Arenabbottella nitens* (Watters, 2013)**
(Figures 19, 96–99)

CHRESONYMY

Abbottella (*Abbottella*) *nitens* Watters, 2013: 7, figs. 1 P–S, 5 R, S, 8 A.

Type Material: Holotype: UF 456806; Paratypes: UF 456808(15), from the type locality.

Type Locality: "Dominican Republic, La Altagracia Province, 16 km S of Higüey, at 100 m. ca. 18.46° N, – 68.71° W."

Distribution and Habitat: Known only from the type locality under rocks among boulders, on a limestone bluff west of Highway 4.

Remarks: Preserved material was not available.

Etymology: L. *niteo*, shine, glitter, in reference to the metallic sheen of most specimens.

***Arenabbottella rosaliae* (Pfeiffer, 1858)**
(Figures 15, 19, 100–103)

CHRESONYMY

Choanopoma rosaliae Pfeiffer *in* Hjalmarson and Pfeiffer, 1858: 139–140, pl. 2, figs. 4–6; Bland, 1861: 355; Pfeiffer, 1865: 111; Pfeiffer, 1876: 161; Kobelt, 1880: 277; Crosse, 1891: 166; Pilsbry, 1933: 130.
Abbottella rosaliae (Pfeiffer, 1858): Henderson and Bartsch, 1920: 75; Bartsch, 1946: 144, 155, pl. 27, figs. 4–6.
Abbottella (*Abbottella*) *rosaliae* (Pfeiffer, 1858): Watters, 2006: 83, 447; Watters, 2013: 14–16, figs. 4 A–E, 9 A.

Type Material: Not located, presumed lost.

Type Locality: "*In insulae Haiti*." Restricted by Watters (2013) to "Dominican Republic, Puerto Plata Province, Loma Catalina."

Distribution and Habitat: This species is known only from Loma Catalina, an outcrop of the Cordillera Septentrional southeast of Sosúa, occurring in ca. 100 km^2. Much of this area is contained in the Parque Nacional El Choco. All specimens seen were found between 30–280 m elevation on limestone bluffs.

Remarks: This species possesses a periostracum although it is lost in most specimens. On fresh examples this periostracum forms short bristles at the junctures of the axial and spiral sculptures. In general, a periostracum appears to be very rare in the Annulariidae.

Etymology: Unknown, the identity of Rosalie has been lost to time.

***Arenabbottella samanensis* (Bartsch, 1946)**
(Figures 19, 104–107)

CHRESONYMY

Abbottella samanensis Bartsch, 1946: 143, 148–149, pl. 25, figs. 7–9.
Abbottella (*Abbottella*) *samanensis* Bartsch, 1946: Watters, 2006: 83, 460; Watters, 2013: 16, figs. 4 F–I, 9 B.

Type Material: Holotype: USNM 504090.

Type Locality: "Cape Samaná, Dominican Republic."

Distribution and Habitat: Samaná Peninsula in the Sierra de Samaná of the Cordillera Septentrional. Live snails have been found in leaf litter.

Remarks: Preserved material was not available.

Etymology: From the Samaná Peninsula.

***Arenabbottella sanchezi* (Bartsch, 1946)**
(Figures 19, 108–113)

CHRESONYMY

Abbottella sanchezi Bartsch, 1946: 143, 149, pl. 26, figs. 1–3.
Abbottella adolphi [*sic*] *peninsularis* Bartsch, 1946: 150–151, pl. 26, figs. 14–16.
Abbottella (*Abbottella*) *adolfi peninsularis* Bartsch, 1946: Watters, 2006: 83, 130; Watters, 2013: 6, 13, figs. 3 J–L, 8 H.
Abbottella (*Abbottella*) *sanchezi* Bartsch, 1946: Watters, 2006: 83, 460; Watters, 2013: 6, 8, 13, 16, 17, figs. 4 J–N, 8 C.

Type Material: *Abbottella sanchezi* Bartsch, 1946: Holotype: USNM 504092. *Abbottella adolphi peninsularis* Bartsch, 1946: Holotype: USNM 504095.

Type Locality: *Abbottella sanchezi* Bartsch, 1946: "2 miles northwest of Sánchez, Dominican Republic."
Abbottella adolphi peninsularis Bartsch, 1946: "On the trail from Samaná to Rio San Juan, Samaná Peninsula."

Distribution and Habitat: The species is found in the Sierra de Samaná from at least Sánchez to Los Cacaos in the south and Las Terrenas in the north. Found in association with limestone boulders, leaf litter, and talus in mesic forests and near caves. All specimens seen were found below 320 m elevation.

Remarks: Bartsch (1946) differentiated *A. sanchezi* and *A. a. peninsularis* based on differences in spire height. Both fall within the range of variation of a single species. This species may exhibit color dimorphism, probably sexual. *Abbottella sanchezi* is here chosen as the valid name for the taxon.

Etymology: *Abbottella sanchezi* Bartsch, 1946: from Sánchez, Dominican Republic. *Abbottella adolphi peninsularis* Bartsch, 1946: from the Samaná Peninsula.

***Arenabbottella sosuaensis* (Bartsch, 1946)**
(Figures 19, 114–117)

CHRESONYMY

Abbottella sosuaensis Bartsch, 1946: 143, 151, pl. 26, figs. 11–13.
Abbottella (*Abbottella*) *sosuaensis* Bartsch, 1946: Watters, 2006: 83, 489–490; Watters, 2010: 17; Watters, 2013: 6, 17, 18, figs. 4 O–S, 9 E.

Type Material: Holotype: USNM 336768.

Type Locality: "Sosúa, 16 miles east of Puerto Plata, Dominican Republic."

Distribution and Habitat: This species is found on the northern slopes of the Cordillera Septentrional from Luperon to Río San Juan under rocks along rolling limestone hills, pastures, and under limestone rubble at the base of cliffs; it may be locally common. It does not occur at El Valle as reported by Watters (2013). All specimens seen were found below 100 m elevation.

Etymology: From Sosúa, Dominican Republic.

***Arenabbottella tenebrosa* (Watters, 2013)**
(Figures 19, 118–121)

CHRESONYMY

Abbottella (*Abbottella*) *tenebrosa* Watters, 2013: 6, 8, figs. 1 U–Y, 8 B.

Type Material: Holotype: UF 456796; Paratypes: UF 456797(15); Paratypes: OSUM 37271(12); Paratypes: BMSM 17937(16), all from the type locality.

Type Locality: "Dominican Republic, Puerto Plata Province, El Choco, near Cabarete. ca. 19.74° N, –70.42° W."

Distribution and Habitat: This species is found from the limestone outcrops of El Choco near Cabarete to just west of Río San Juan. All specimens seen were found below 20 m elevation.

Etymology: L. *tenebrosus*, dark, gloomy, in reference to the shell color.

?*Arenabbottella tentorium* (Pfeiffer, 1850)
(Figures 74, 75)

CHRESONYMY

Cyclostoma tentorium Pfeiffer, 1850: 77; Pfeiffer, 1854b: 284, pl. 38, figs. 16–18; Reeve, 1862: pl. 22, fig. 145.
Choanopoma tentorium (Pfeiffer, 1850): Pfeiffer, 1851: 155; Pfeiffer, 1852a: 168; Pfeiffer, 1852b: 27; Pfeiffer, 1853: 118; Adams and Adams, 1856: 296; Pfeiffer, 1858b: 102; Bland, 1861: 355; Pfeiffer, 1865: 111; Pfeiffer, 1876: 161; Kobelt, 1880: 277; Crosse, 1891: 167.
Abbottella (*Abbottella*) *tentorium* (Pfeiffer, 1850): Watters, 2006: 83, 505.
non Abbottella tentorium (Pfeiffer, 1850): Henderson and Bartsch, 1920: 75; Bartsch, 1946: 144, 153, pl. 27, figs. 1– 3 [= ?*A. wetmorei*].

Type Material: Not located, presumed lost.

Type Locality: "*in insula Haiti*."

Remarks: Pfeiffer's 1850 description of "*Interdum rubro-punctata*" does not conform to any known *Abbottella*. Reeve's 1862 figure seems to show this feature more so than does Pfeiffer's 1854 figure. At 6.5 mm in diameter only *M. diadema* and *A. urbana* are smaller. Bartsch's 1946 specimen (his pl. 27, figs. 1–3) from an unknown locality does not seem to be the same species and lacks any red spots; it appears to be a pale specimen of *A. wetmorei*. This may possibly be an earlier name for *A. urbana*.

Etymology: L. *tentorium*, a tent, a noun in apposition.

***Arenabbottella urbana* (Watters, 2012)**
(Figures 19, 122–128)

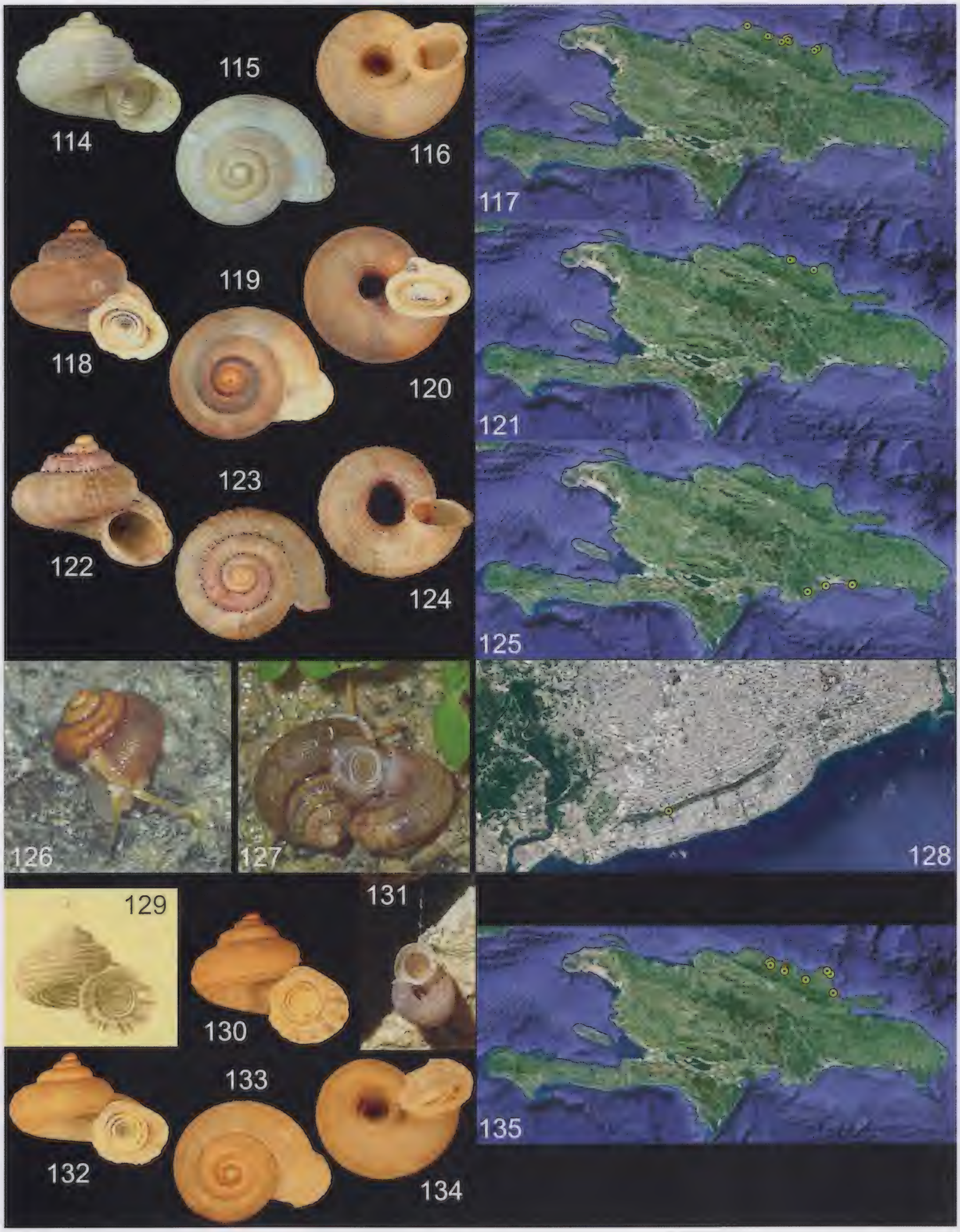
CHRESONYMY

Abbottella (*Abbottella*) *urbana* Watters, 2012: 1, 3, figs. 1–3; Watters, 2016: 115–166.

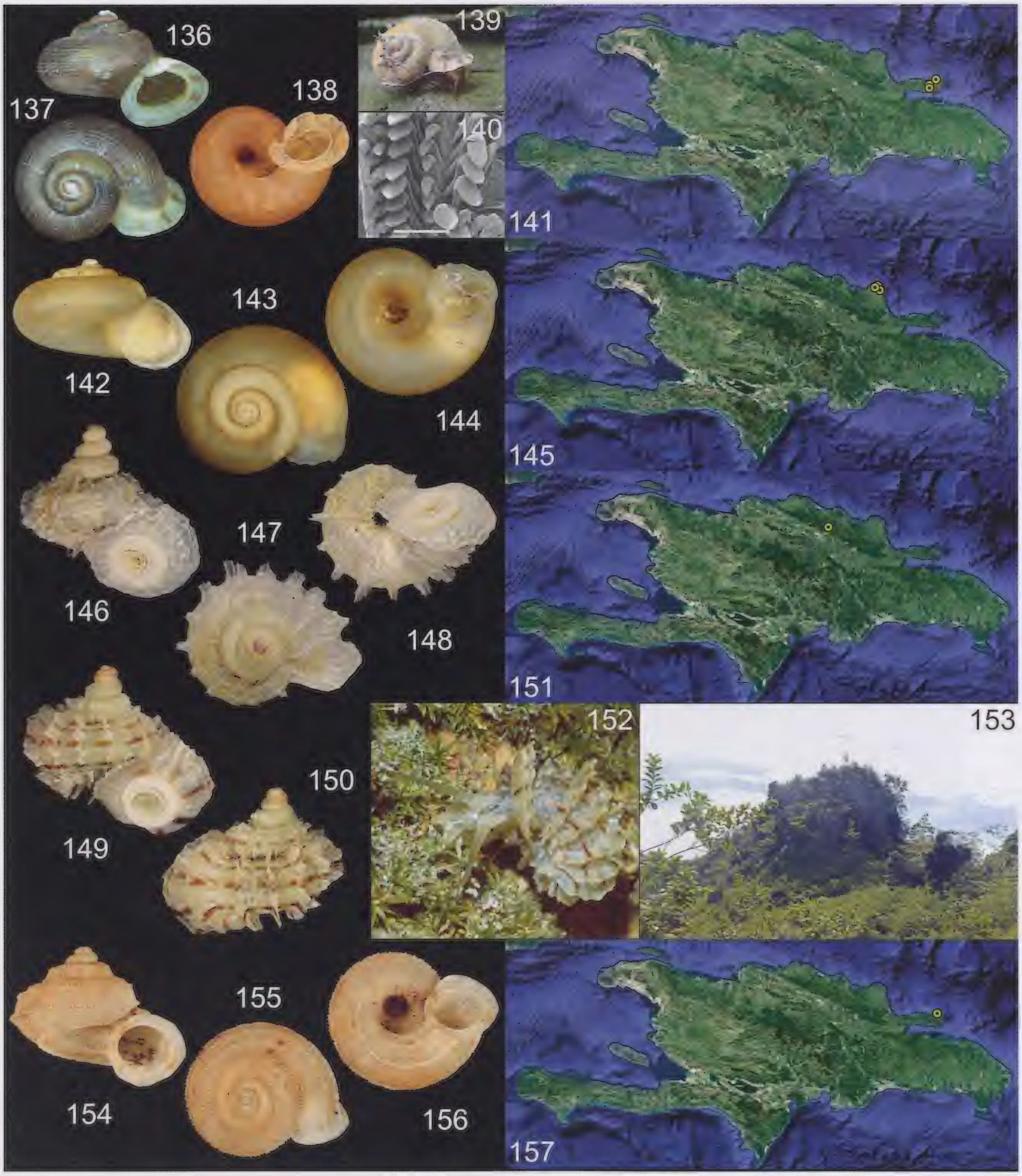
Type Material: Holotype: UF 446061; Paratype: OSUM 36509(1), from the tdype locality.

Type Locality: "Parque Central, off José Contreras Blvd., N of the Loteria barrio of western Santo Domingo, Distrito Nacional, Dominican Republic, 18.44 N, –69.97 W."

Distribution and Habitat: Known from Parque Central/ Parque Mirador del Sur in downtown Santo Domingo



Figures 114–135. *Arenabbottella*. **114–117.** *Arenabbottella sosuaensis* (Bartsch, 1946). **114, 115. Holotype**, USNM 336768 (7.0 mm diameter). **116.** UF 218136 (6.9 mm diameter). **117.** Distribution map. **118–121.** *Arenabbottella tenebrosa* (Watters, 2013). **118–120. Holotype**, UF 456796 (8.9 mm diameter). **121.** Distribution map. **122–128.** *Arenabbottella urbana* (Watters, 2012). **122–124. Holotype**, UF 446061 (4.9 mm diameter). **125.** Distribution map. **126.** Live individual (photos ©S. Aiken). **127.** Mating pair (photos ©S. Aiken). **128.** Type locality in Parque Central in Santo Domingo. **129–135.** *Arenabbottella wilhelmi* (Pfeiffer, 1858). **129.** *Choanopoma wilhelmi* Pfeiffer *in* Hjalmarson and Pfeiffer, 1858: pl. 2, fig. 3. **130.** UF 216150 (8.0 mm diameter). **131.** Live individual suspended from mucus thread. **132–134.** UF 216150 (8.5 mm diameter). **135.** Distribution map.



Figures 136–157. *Lagopoma*, *Leiabbottella*, *Meganiphe*, *Microabbottella*. **136–141.** *Lagopoma lagopoma* Bartsch, 1946. **136–137. Holotype**, USNM 356198 (5.0 mm diameter). **138.** GTW 10081a (9.7 mm diameter). **139.** Live individual. **140.** Radula (bar=100μ). **141.** Distribution map. **142–145.** *Leiabbottella galaxius* Watters, 2010. **142–144. Paratype**, OSUM 35491 (8.4 mm diameter). **145.** Distribution map. **146–153.** *Meganiphe rhecta* Thompson, 1978. **146–148. Paratype**, GTW 8227a (10.6 mm diameter). **149–150.** GTW 11371b (8.0 mm diameter). **151.** Distribution map. **152.** Live individual (photo ©S. Aiken). **153.** Habitat (photo ©S. Aiken). **154–157.** *Microabbottella diadema* (Watters, 2013). **154–156. Holotype**, UF 456814 (6.0 mm diameter). **157.** Distribution map.

(Figure 128), among vacant lots in Boca Chica to the east, and almost to Peravia Province to the west. It is likely that this species historically occurred along the southern extent of Santo Domingo Province, which is now heavily developed. It still exists in remaining pockets of suitable habitat scattered throughout the region, including local land fills. It has been found under limestone rubble.

Etymology: L. *urbana*, of a city.

Arenabbottella wilhelmi (Pfeiffer, 1858)
(Figures 19, 129–135)

Chresonymy

Choanopoma wilhelmi Pfeiffer *in* Hjalmarson and Pfeiffer, 1858: 139, pl. 2, figs. 1–3; Bland, 1861: 355; Pfeiffer, 1865: 110–111; Pfeiffer, 1876: 161; Kobelt, 1880: 277; Crosse, 1891: 165–166.
Abbottella wilhelmi (Pfeiffer, 1858): Henderson and Bartsch, 1920: 75; Bartsch, 1946: 143, 144, pl. 24, figs. 1–3.
Abbottella (*Abbottella*) *wilhelmi* (Pfeiffer, 1858): Watters, 2006: 83, 549; Watters, 2013: 13, 16, 17, figs. 4 T–X, 8 D.

Type Material: Not located, presumed lost.

Type Locality: "*In insulae Haiti.*" Pfeiffer continued that it "was collected under stones in moist places near Puerto Plata" [German translation].

Distribution and Habitat: This species occurs on the northern slopes of the Cordillera Septentrional from Puerto Plata to Nagua, including Pico Isabel de Torres, Loma Blanca at El Choco, and the north side of the outcrop between Río San Juan and Cabrera. Individuals are found from cloud forests to open, disturbed areas under limestone rubble.

Remarks: This species has been found suspending itself from mucus threads (Figure 131).

Etymology: Probably Rudolph Wilhelm Dunker (1809–1885), German conchologist.

Genus *Lagopoma* Bartsch, 1946

Type species: *Lagopoma lagopoma* Bartsch, 1946, by original designation.

Description: Shells small (ca. 9 mm in diameter), depressed turbinoid, sculpture of minute pustules on more-or-less weak spiral cords, cords more prominent in umbilicus, suture channeled, outer lip expanded, auriculate. Lip folded posteriorly and conspicuously notched. Radula as in subfamily (Figure 140).

Distribution: Samaná Peninsula of Dominican Republic (Figure 21). Snails live under leaf litter, limestone rubble, and on wet outcrops in mesic forests.

Remarks: Bartsch (1946) established *Lagopoma* as a monotypic genus characterized by a folded and notched outer lip. The enrolled lip also occurs in *Arenabbottella samanaensis* and *Abbottipoma gabbi*. In this study *Lagopoma* was found to be sister to *Abbottipoma*, and like that genus is endemic to the Samaná Peninsula.

***Lagopoma lagopoma* Bartsch, 1946**
(Figures 21, 136–141)

Chresonymy

Lagopoma lagopoma Bartsch, 1946: 142–143, pl. 23, figs. 1–3; Watters, 2006: 92, 324; Watters, 2013: 18, figs. 4 Y–CC, 8E.

Type Material: Holotype: USNM 356198 (2 specimens in lot, holotype listed as 5.0 mm long specimen).

Type Locality: "Laguna, 4 miles N of Samaná, Samaná Province, Dominican Republic."

Distribution and Habitat: Occurs on the limestone outcrop of the Sierra de Samaná that occupies the northeastern-most prominence, from El Valle to Loma Travesada. This species is found in association with *A. abbotti*.

Comparison with Other Species: This species is characterized by the peculiar folded auricle and notched outer lip.
Arenabbottella samanaensis and *Abbottipoma gabbi* occasionally have a similar auricle but lack the notch.

Etymology: Sp. *lago*, lake, lagoon + *-poma*, a standard ending for annulariid genera. The type was collected at Laguna.

***Leiabbottella* Watters, 2010**

Type species: *Leiabbottella galaxius* Watters, 2010, by original designation.

Description: Shells small (ca. 10 mm in diameter), nearly planispiral, sculptureless except for microscopic axial threads and faint spiral ridges in umbilicus, outer lip narrowly expanded.

Distribution: Endemic to an outcrop of the Villa Trina Formation of the Río San Juan complex (Figure 21).

Remarks: In this phylogenetic study *Leiabbottella galaxius*, the type species, was a weakly supported member of the *Arenabbottella* clade. Conchologically it is very dissimilar from *Arenabbotella* species. At the risk of

perpetuating a possibly paraphyletic genus, we maintain *Leiabbottella* as a distinct genus pending further study. However, other smooth- shelled taxa previously assigned to *Leiabbottella* (*soluta* and *thompsoni*) are unrelated and are reassigned to the new genus *Preclaripoma*. Conchologically they differ primarily in the greatly expanded outer lip, which is very narrow in *L. galaxius*. The lack of shell sculpture appears to be convergent between the two groups.

Etymology: G. *leios*, smooth + *Abbottella*.

***Leiabbottella galaxius* Watters, 2010**
(Figures 21, 142–145)

CHRESONYMY

Leiabbottella galaxius Watters, 2010: 17–19, pl. 1, figs. 5, 6; Watters, 2013: 10, 18-19, figs. 2 J–L, 8 F.

Type Material: Holotype: UF 434779; Paratype: UF 434780(1); Paratypes: BMSM 17972(2); Paratype: OSUM 35491(1), all from the type locality.

Type Locality: "Dominican Republic, Samaná Province, Samaná Peninsula, along Rt. 5 between Santa Bárbara de Samaná and Sánchez, in the southern foothills of the Sierra de Samaná." However, subsequent extensive collections in the area of the original type locality have failed to find this species. All other records place it exclusively on an outcrop of the Villa Trina Formation between Río San Juan and Cabrera. It seems certain that the original type locality was a mislabled lot and in error. The type locality is here corrected to "outcrop 0.5 km NNE of Caro Clara, María Trinidad Sánchez Province, Dominican Republic."

Distribution and Habitat: Endemic to an outcrop of the Villa Trina Formation of the Río San Juan complex, an area < 150 km^2. This is undifferentiated limestone, siltstone, and marl of Upper Miocene–Lower Pliocene age (Draper et al., 1991). All specimens seen were found from sea level to 30 m elevation. At Abreu, individuals were found within several meters of the sea at <1 m elevation.

Etymology: Gr. *galaxius*, an allusion to having the appearance of the Milky Way Galaxy.

Genus *Meganiphe* Thompson, 1978

Type Species: *Meganiphe rhecta* Thompson, 1978, by original designation.

Description: Shell small (8–10 mm in diameter), turbinate, whorls adnate, nondecollate. Moderately wide umbilicus. Axial sculpture of distantly spaced, greatly expanded, erect and undulating lamellae, ca. 12–14 on final whorl. Spiral sculpture absent. Aperture circular, lip greatly expanded rather evenly but less so facing body whorl, barely separated from body whorl, composed of numerous greatly expanded lamellae, gently reflected abaperturally, undulating, weakly auriculate. Operculum multispiral with erect, calcareous lamella that is reflected to form almost flat plate. Radula as in subfamily.

Distribution: Endemic to Loma del Puerto (Figures 18, 153fig10).

Remarks: *Meganiphe* is apparently a narrowly endemic, monotypic genus. It is most closely related to *Rolleia*, which occurs in the same high elevation habitats. This appears to be an offshoot of *Rolleia* with exaggerated sculpture.

Etymology: L. *mega*, giant + G. *nipha*, snowflake.

***Meganiphe rhecta* Thompson, 1978**
(Figures 19, 146–153)

CHRESONYMY

Meganiphe rhecta Thompson, 1978: 43–48, figs. 1–4; Abbott, 1989: 53; Watters, 2006: 92, 441–442; Aiken, 2018: 4–9.

Type Material: Holotype: UF 22745; Paratypes: UF 22746(1), 22747(1); Paratype: USNM 711132(6); Paratype: GTW 8227a(1).

Type Locality: "Dominican Republic, Puerto Plata Province, Loma del Puerto, Yaroa, 700 m elevation." This site appears to be on the border between Santiago and Puerto Plata provinces.

Distribution and Habitat: This beautiful species is apparently endemic to Loma del Puerto. This is a portion of the La Piedra Member of the Villa Trina Formation. It is characterized by massive, cliff-forming reefal limestone of Upper Miocene–Lower Pliocene age (Zoeten et al., 1991). The habitat is a 700–800 m elevation, nearly inaccessible ridge in a cloud forest, on limestone blocks with lichens, moss, and ferns (Aiken, 2018, and figures).

Remarks: Shells may be banded or not. This species co-occurs with the lizard *Anolis distichus ignigularis* Mertens, 1939, which may be predaceous on them (Aiken, 2018).

Etymology: Gr. *rhecta*, brittle. *Meganiphe rhecta* – Brittle Giant Snowflake.

Genus *Microabbottella* new genus

Type species: *Abbottella* (*Abbottella*) *diadema* Watters, 2013.

Description: Shell minute (4–6 mm in diameter), turbinate, whorls adnate except just before lip. Umbilicus wide. Protoconch of ca. 1.5 minutely pustulose whorls but demarcation between protoconch and teleoconch not well- defined. Teleoconch of 2.5–2.75 whorls. Axial sculpture of numerous, crowded, low lamellae. Spiral sculpture present only as keels. The axial sculpture on keels forms very dense, finely serrate edge. Aperture double, circular, solute from final whorl. Inner lip smooth, narrowly exserted. Outer lip slightly expanded, consisting of numerous fused lamellae, with two low auricles 180° apart. Operculum multispiral with oblique, erect, calcareous lamella. Radula and anatomy unknown.

Distribution: Endemic to Loma Travesada (Figure 20).

Remarks: This genus has the smallest shells of any abbottellines and has the fewest number of teleoconch whorls (<3); the shells are also among the smallest known annulariids. The curious combination of tightly packed axial sculpture and prominent spiral cords is unlike any other annulariid. Currently this is a monotypic genus. Although preserved material was not available for phylogenetic work, the unique conchological features indicate a genus apart from other abbottellines. Its apparently very limited range on a single hill in the eastern–most Samaná Peninsula suggests it may have evolved in isolation there when the peninsula was still an island.

Etymology: L. *micro*, very small + *Abbottella*.

***Microabbottella diadema* (Watters, 2013)**
(Figures 20, 154–157)

Chresonymy

Abbottella (*Abbottella*) *diadema* Watters, 2013: 4, 6, figs. 1 F–J, 5 P, 7 B.

Type Material: Holotype, UF 456814; Paratypes: UF 456815(5), from the type locality.

Type Locality: "Dominican Republic, Samaná Province, Cabo Cabrón, at 280 m. ca. 19.34° N, –69.25° W."

Distribution and Habitat: Known only from the type locality at the isolated Loma Travesada of the Sierra de Samaná under limestone boulders on a slope in virgin rain forest; abundant. It may occur in <10 km^2.

Etymology: Gr. *diadema*, headband, crown.

Genus *Preclaripoma* new genus

Type Species: *Leiabbottella thompsoni* Watters, 2013.

Description: Shells large for subfamily (9–15 mm in diameter), nearly planispiral, sculptureless except for microscopic axial threads and faint spiral ridges in umbilicus. Outer lip greatly expanded. Operculum as in subfamily.

Distribution: The few records indicate isolated localities in the Cordillera Septentrionale and the Los Haitises of the Majugual area (Figure 21).

Remarks: Originally considered members of *Leiabbottella*, results here indicate these taxa are unrelated to that genus and constitute a new taxon. The lack of sculpture seen in *Leiabbottella* and *Preclaripoma* is convergent. *Preclaripoma* is weakly supported as a sister group of *Abbottella*. These are very rare species in collections.

Etymology: L. *preclarus*, very beautiful, splendid + *-poma*.

Key to Species

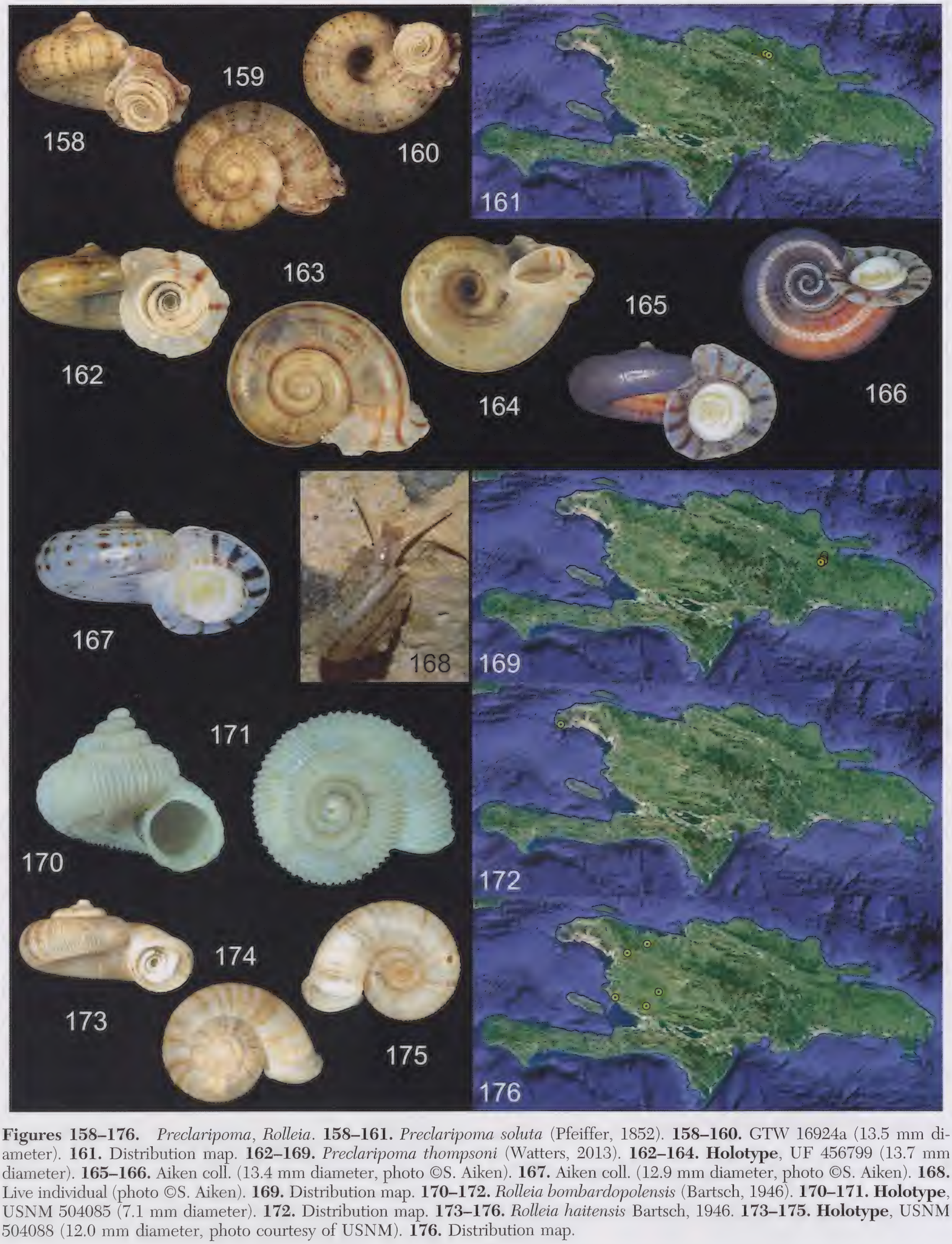
1) Whorls ca. 3× as high as wide, outer lip barely adnate to preceding whorl ..... *soluta*
1) Whorls ca. 4× as high as wide, outer lip broadly adnate to preceding whorl ..... *thompsoni*

***Preclaripoma soluta* (Pfeiffer, 1852)**
(Figures 21, 158–161)

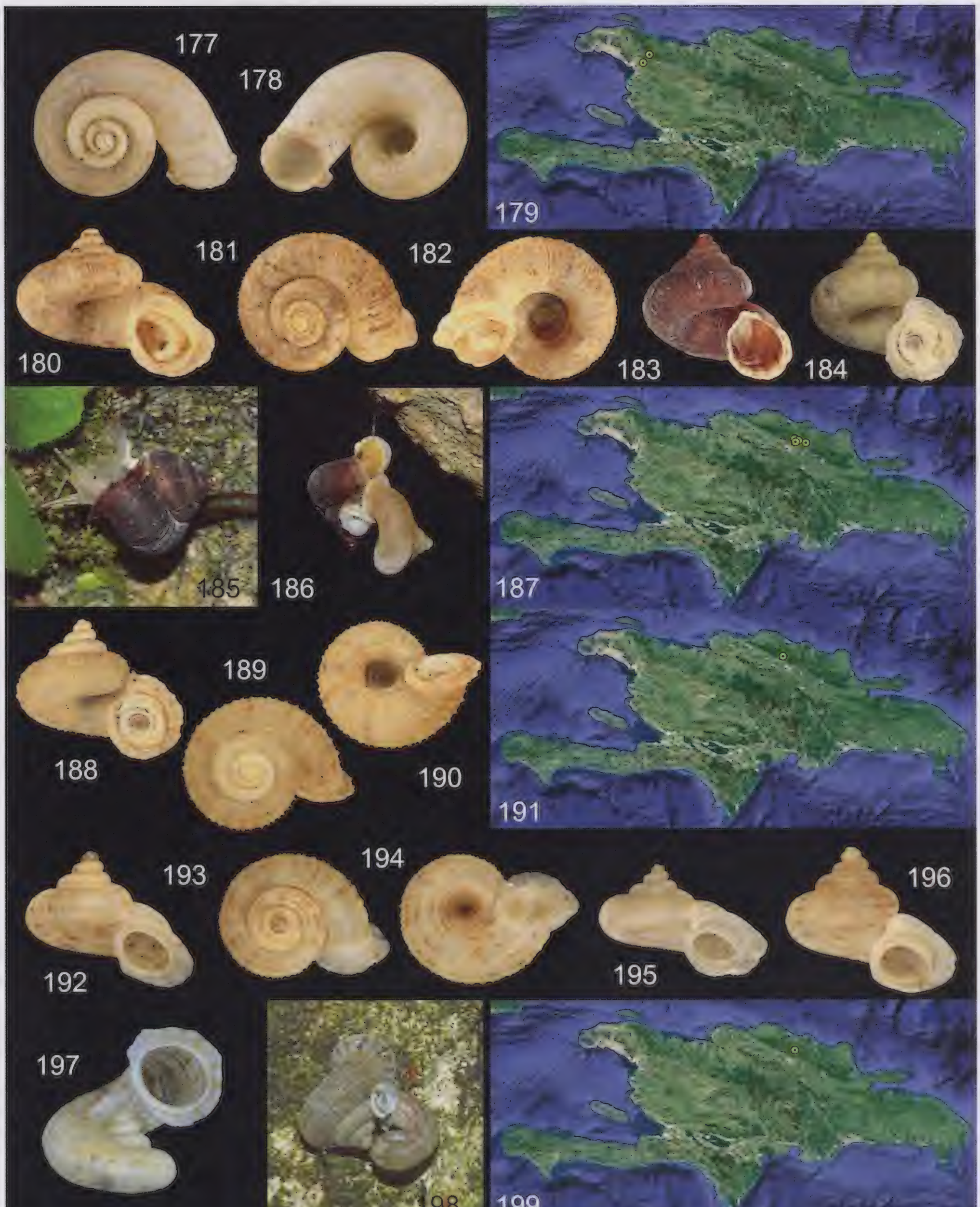
Chresonymy

Choanopoma solutum "Richard" Pfeiffer, 1851: 155 [*nomen nudum*]; Adams and Adams, 1856: 296; Hjalmarson and Pfeiffer, 1858: 138–139; Bland, 1861: 355; Pfeiffer, 1865: 110; Pfeiffer, 1876: 160; Crosse, 1891: 169.
Choanopoma? *solutum* "Richard:" Pfeiffer, 1852a: 167; Pfeiffer, 1853: 117; Pfeiffer, 1858b: 102.
Cyclostoma solutum ("Richard"): Pfeiffer, 1854b: 295, pl. 39, figs. 8–10; Pfeiffer, 1858a: 188.
Cyclostoma (*Choanopoma*) *solutum* "Richard" Pfeiffer, 1852: Shuttleworth, 1856: 261–263, 270.
Cyclostoma solutum "Richard" Pfeiffer, 1852: Reeve, 1862: pl. 23, figs. 160a,b.
Choanopoma solutum "Richard" Pfeiffer, 1852: Kobelt, 1880: 277.
Abbottella solutum (Pfeiffer, 1852): Henderson and Bartsch, 1920: 75.
Choanopoma (*Abbotella* [*sic*]) *solutum* "Richard" Pfeiffer, 1852: Clench and Aguayo, 1937: 67.
Incertipoma solutum (Pfeiffer, 1852): Bartsch, 1946: 171, 173–174, pl. 30, figs. 2–4.
Rolleia ? *soluta* (Pfeiffer, 1852): Watters, 2006: 93, 487–488.
Leiabbottella soluta (Pfeiffer, 1852): Watters, 2010: 18, 19; Watters, 2013: 9, 11, 17, figs. 2 F–I, 7 D; Aiken, 2018: 7.

Type Material: ? NHMUK, not located, but in Cuming collection, *fide* Shuttleworth, 1856: 262.



Figures 158–176. *Preclaripoma*, *Rolleia*. **158–161.** *Preclaripoma soluta* (Pfeiffer, 1852). **158–160.** GTW 16924a (13.5 mm diameter). **161.** Distribution map. **162–169.** *Preclaripoma thompsoni* (Watters, 2013). **162–164. Holotype**, UF 456799 (13.7 mm diameter). **165–166.** Aiken coll. (13.4 mm diameter, photo ©S. Aiken). **167.** Aiken coll. (12.9 mm diameter, photo ©S. Aiken). **168.** Live individual (photo ©S. Aiken). **169.** Distribution map. **170–172.** *Rolleia bombardopolensis* (Bartsch, 1946). **170–171. Holotype**, USNM 504085 (7.1 mm diameter). **172.** Distribution map. **173–176.** *Rolleia haitensis* Bartsch, 1946. **173–175. Holotype**, USNM 504088 (12.0 mm diameter, photo courtesy of USNM). **176.** Distribution map.



Figures 177–199. *Rolleia*. **177–179.** *Rolleia martensi* (Maltzan, 1888). **177–178.** Possible **syntype**: ZMB 40725 (15 mm diameter, photo courtesy Malacological Collection, Museum für Naturkunde Berlin, Leibniz Institute for Research in Evolution and Biodiversity at the Humboldt University, photography L. Maitas). **179.** Distribution map. **180–187.** *Rolleia oberi* Watters and Duffy, 2010. **180–182.** Holotype UF 434775, 10.3 mm diameter. **183.** GTW 14180b (7.3 mm diameter). **184.** GTW 14180b (8.6 mm diameter). **185.** Live individual (photo ©S. Aiken). **186.** Mating pair suspended on mucous threads (photo ©S. Aiken). **187.** Distribution map. **188–191.** *Rolleia paradoxa* (Watters, 2013). **188–190. Holotype**, UF 456812 (7.8 mm diameter). **191.** Distribution map. **192–199.** *Rolleia simonaikeni* **new species**. **192–194.** Holotype, OSUM 46107 (9.6 mm diameter). **195. Paratype**, UF 525639 (9.0 mm diameter). **196. Paratype**, BMSM 128507 (10.6 mm diameter). **197.** Hyperstrophic individual (8.2 mm length, photo ©S. Aiken). **198.** Mating pair (photo ©S. Aiken). **199.** Distribution.

Type Locality: "Island of Santo Domingo." Originally restricted by Watters (2012) to "the southern edge of Los Haitises Mountains, N of Majagual, ca. 12 km NW of Sabana Grande de Boyá, Monte Plata Province, Dominican Republic." However, this was found to be a different species described as *Leiabbottella thompsoni* Watters, 2013. The type locality was corrected by Watters (2013) to "Yásica Abajo, Puerto Plata Province, Dominican Republic."

Distribution and Habitat: Known only from the region of Loma del Puerto near Lajas de Yaroa and Gurabito de Yaroa in the Cordillera Septentrional, between Puerto Plata and Santiago de Los Caballeros; ca. 500–900 m elevation. It lives in the soil under rocks (Aiken, 2018).

Remarks: This species occurs at higher elevations than *P. thompsoni,* up to at least 900 m.

Etymology: L. *solutus*, dissolved; possibly used here to refer to the openly coiled whorls.

***Preclaripoma thompsoni* (Watters, 2013)**
(Figures 21, 162–169)

Chresonymy

Leiabbottella thompsoni Watters, 2013: 9–11, 17, 18, figs. 2 A–E, 7 E.

Type Material: Holotype: UF 456799; Paratypes: UF 236225(91), from the type locality.

Type Locality: "Dominican Republic, Monte Plata Province, 5 km N of Majagual [Majugual], at 150 m. ca. 19.09° N, –69.83° W."

Distribution and Habitat: Found in the karstic region of Los Haitises between the Cordillera Central and the Cordillera Oriental around Guaragao and Majugual on and at the base of limestone knolls and in ravines in mesic forests under debris and leaf litter. The Majugual region is the western part of the Cevicos Formation, composed of karsted, massive limestone blocks of Upper Miocene–Lower Pliocene age (Draper and Lewis, 1991). All specimens seen were found between 100–320 m elevation. Locally common.

Etymology: Named for the late Dr. Fred Thompson, Curator, UF, who collected the types.

Genus *Rolleia* Crosse, 1891

Type Species: *Cyclotus martensi* Maltzan, 1888, by original designation.

Petasipoma Bartsch, 1946, is a synonym.

Description: Shell medium-sized for family (8–15 mm in diameter), depressed to turbinoid, terminal portion of final whorl solute from previous whorl and may be deflected anteriorly. Axial sculpture of numerous close-set, very fine threads or low lamellae. Spiral sculpture as weak cords that may be limited to umbilicus or may be entirely absent. Outer lip widely expanded in most species.

Distribution: Specimens are very rare in collections and the ranges of the species are not well-known. All appear to be upland species in the Massif du Nord and Montagnes Noires of Haiti and the Cordillera Septentrional of the Dominican Republic (Figure 20). These highlands are largely unexplored and nearly impenetrable. Given the amount of endemism in this group, it is to be expected that other species undoubtedly await discovery.

Remarks: The Haitian species may be unrelated to those from the Dominican Republic. *Paradoxa* and *bombardopolensis* also may constitute a separate genus but require additional material.

Etymology: Hermann Rolle (f. 1887–1911), German shell dealer.

Key to Species

1) Operculum fits within aperture, spiral sculpture absent or present only in umbilicus 2
1) Operculum too large to fit in aperture, spiral sculpture of weak cords over whorls 5

2) Shell nearly smooth, final portion of last whorl widely solute ..... *martensi*
2) Shell with coarser axial sculpture, final portion of last whorl narrowly solute 3

3) Outer lip narrowly expanded ..... *haitensis*
3) Outer lip widely expanded 4

4) Axial sculpture close-set and barely separated by width of thread ..... *oberi*
4) Axial sculpture separated by gaps several times wider than thread ..... *simonaikeni*

5) Outer lip widely expanded and notched .... *paradoxa*
5) Outer lip narrowly expanded and complete ..... *bombardopolensis*

***Rolleia bompardopolensis* (Bartsch, 1946)**
(Figures 20, 170–172)

Chresonymy

Petasipoma bombardopolense Bartsch, 1946: 138–139, pl. 21, figs. 4-6.
Abbottella (*Petasipoma*) *bombardopolensis* (Bartsch, 1946): Watters, 2006: 84, 179.
Abbottella (*Gundlachtudora*) *bompardopolensis* (Bartsch, 1946): Watters, 2013: 17–18, figs. 1 DD, 8 I.

Type Material: Holotype: USNM 504085 (2 specimens in lot, holotype listed as 6.5 mm long specimen).

Type Locality: "Crevices in rocks in a ravine a little west of Bombardopolis, Haiti."

Distribution and Habitat: *Rolleia bombardopolensis* is known from Bombardopolis and Terre Neuve in the western-most extent of the Cordillera Centrale in Haiti. Its habitat is unknown.

Remarks: The structure of the operculum, which is nearly flat and cannot be withdrawn into the aperture, separates this from all other abbottellines except *R. paradoxa*. The shell sculpture of both is consistent with *Rolleia* and the species occupy the known range of *Rolleia* but their assignment here is highly conjectural. No suitable preserved material was available. The opercular features are here considered a species-level characteristic. The Cuban species *decolorata* Pfeiffer, 1859, is maintained in Bartsch's subgenus *Gundlachtudora* but probably belongs to the Abbottellinae as well.

Etymology: From Bombardopolis, Haiti.

***Rolleia haitensis* Bartsch, 1946**
(Figures 20, 173–176)

Chresonymy

Rolleia haitensis Bartsch, 1946: 140, 141–142, pl. 23, figs. 7–9; Watters, 2006: 93, 288; Watters and Duffy, 2010b: 187, figs. 7–9; Watters, 2013: 20, 22, figs. 5 A–F, 7 I.

Type Material: Holotype: USNM 504088.

Type Locality: "Ennery, Haiti."

Distribution and Habitat: It is known from the Montagnes Noires range of Haiti. Its habitat is unknown.

Remarks: It is possible that more than one species has been treated under this name.

Etymology: From Haiti.

***Rolleia martensi* (Maltzan, 1888)**
(Figures 20, 177–179)

Chresonymy

Cyclotus martensi Maltzan, 1888: 179.
Rolleia martensi (Maltzan, 1888): Crosse, 1891: 163–164, pl. 2, fig. 4; Wenz, 1939: 550, fig. 1471; Bartsch, 1946: 140–141, pl. 23, figs. 4–6; Watters, 2006: 93, 349; Watters and Duffy, 2010b: 187, figs. 10, 11; Watters, 2013: 20.
Rolleia martensii [*sic*] (Maltzan, 1888): Thiele, 1929: 134.

Type Material: Possible **syntype**: ZMB 40725.

Type Locality: "*Sanssouci in parte meridionali insulae Haiti.*" Bartsch (1946: 141) gave "Plaisance, the type locality." This is incorrect; the Sans-Souci Palace is located in Milot, 27 km east of Plaisance.

Distribution and Habitat: This rarely seen species is found in the Massif du Nord and Montagnes Noires of Haiti. Habitat information is lacking.

Etymology: Karl Eduard von Martens (1831–1904), German conchologist at Museum für Naturkunde, Berlin.

***Rolleia oberi* Watters and Duffy, 2010**
(Figures 20, 180–187)

Chresonymy

Rolleia oberi Watters and Duffy, 2010b: 185, 187, figs. 1–6; Watters, 2013: 20, 22, figs. 5 G–N, 8 G; Aiken, 2018: 7.

Type Material: Holotype: UF 434775; Paratypes: UF 434776(3); Paratypes: BMSM 17970(2); Paratypes: OSUM 35489(2), all from the type locality.

Type Locality: "On road half way between Santiago de los Caballeros and Puerto Plata, El Puerto, La Has, Puerto Plata Province, Dominican Republic, at 830–1000 m in the Cordillera Septentrional." This road is Carretera Turistica Gregorio Luperon.

Distribution and Habitat: This species is probably limited to the area of Loma del Puerto between Puerto Plata and Santiago de Los Caballeros in the Cordillera Septentrional. All specimens seen were found between 700–800 m elevation on limestone outcrops in cloud forest.

Remarks: As with a few other abbottellines (and helicinids), this species is found in two different colors – brown and yellow/white. This may be a sexual characteristic with males being the yellow/white morph. This species has been observed suspending itself from mucus thread(s) (Figure 186).

Etymology: Jim Ober, collector of the types.

***Rolleia paradoxa* (Watters, 2013)**
(Figures 20, 188–191)

Chresonymy

Abbottella (*Gundlachtudora*) *paradoxa* Watters, 2013: 8, 9, 18, figs. 1 Z–CC, 9 F.

Type Material: Holotype: UF 456812; Paratypes: UF 456813(22), from the type locality.

Type Locality: "Dominican Republic, Santiago Province, Loma Diego de Ocampo, at 1200 m. ca. 19.62° N, - 70.76° W."

Distribution and Habitat: Known only from Loma Diego de Ocampo of the Cordillera Septentrional, on limestone rocks on the mountain crest in dense forest with thick vegetative debris, mosses, and epiphytes. Loma Diego de Ocampo is located north of Santiago de Los Caballeros and is the highest point of the Cordillera Septentrional at 1,200 m.

Remarks: Watters (2013) placed this species under *Gundlachtudora* based on opercular features. However, the shell sculpture is unlike that genus but more similar to *Rolleia*. See Remarks under *Rolleia bombardopolensis*.

Etymology. L. *paradoxus*, strange, contrary to expectation.

***Rolleia simonaikeni* new species**
(Figures 20, 192–199)

CHRESONYMY

Rolleia sp. Aiken, 2018: figs. top of p. 8.

Description: Shell small (largest specimen seen, 11.0 mm in diameter including outer lip; smallest seen, 8.0 mm in diameter including outer lip; holotype 9.6 mm in diameter including outer lip), depressed turbinoid, widely umbilicate. Whorls adnate except for just behind outer lip. Nuclear whorls 1.5, smooth, minute, white or brown, weakly demarcated from teleoconch whorls. Teleoconch whorls 3. Axial sculpture of minute, low, erect lamellae (90–100 on final whorl), evenly produced all around, more or less evenly distributed but closer set near lip, with microscopic threads between some lamellae. Spiral sculpture absent. Aperture deflected anteriorly. Outer lip very broadly expanded, narrower facing umbilicus, just touching previous whorl, somewhat concave posteriorly, composed of numerous fused lamellae, with wide posterior auricle. Inner lip round, exserted, projecting beyond outer lip. Shell white or pale tan with ca. 9 spiral bands of smudged tan spots or dashes that show through into aperture. Operculum not preserved with specimens but based on photographs of live animals (Aiken, 2018), composed of single, reflected spiral lamella. Radula unknown. Preserved material was not available for phylogenetic analysis.

Type Material: Holotype: OSUM 46107 (9.6 mm in diameter); **Paratypes:** UF 525639(1), 9.0 mm in diameter; BMSM 128507 (1), 10.6 mm in diameter.

Additional Material: GTW 17281a(1); Aiken coll. (29), all from the type locality.

Type Locality: Dominican Republic, Santiago Province, Loma del Puerto, 1.4 km NNW of Lajas de Yaroa.

Distribution and Habitat: Known only from a crevice in a single house-sized limestone block on Loma del Puerto at 685 m elevation in a cloud forest. This is a portion of the La Piedra Member of the Villa Trina Formation. It is characterized by massive, cliff-forming, reefal limestone of Upper Miocene–Lower Pliocene age (Zoeten et al., 1991).

Remarks: This species may occupy the narrowest range of any annulariid, having been found only in a single fissure on a single small outcrop (Aiken, 2018). It is also unique in having the only known dextral hyperstrophic example recorded for the family (Figure 197).

Etymology: Named for Simon Aiken (UK), collector of the types and generous contributor to this and other studies.

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Appendix 1. Specimens used in phylogenetic study. DR = Dominican Republic.

Appendix 1

Taxon	GenBank (COI/ 12S/ H3)	Source Accession	Locale
Abbottella crataegus (Watters, 2016)	MT119707/ NA/ NA	GTW 16492c	Majugual, DR
Abbottella moreletiana (Crosse, 1873)	MT119681/ MT119719/ MT119733	GTW 7071g	Boca del Infierno, DR
Abbottella domingoensis (Bartsch, 1946)	MT119706/ MT119717/ MT119734	GTW 16491c	Rio Naranjo, DR
Abbottella domingoensis (Bartsch, 1946)	MT119705/ MT119718/ NA	GTW 16491b	Puerto Bonito, DR
Abbottipoma abbotti (Bartsch, 1946)	MT119695/ MT119723/ NA	GTW 10829b	El Valle, DR
Abbottipoma abbotti (Bartsch, 1946)	MT119696/ MT119724/ NA	GTW 10829c	El Valle, DR
Abbottipoma crossei (Bartsch, 1946)	MT119691/ MT119726/ MT119730	GTW 9432b	Anadel, DR
Abbottipoma crossei (Bartsch, 1946)	MT119692/ NA/ NA	GTW 9432c	Talanquera, DR
Arenabbottella mellosa (Watters and Duffy, 2010)	MT119679/ NA/ NA	GTW 7020f	Río San Juan, DR
Arenabbottella rosaliae (Pfeiffer, 1858)	MT119712/ MT119722/ NA	GTW 16507b	Cabarete, DR
Arenabbottella rosaliae (Pfeiffer, 1858)	MT119713/ NA/ NA	GTW 16507c	Monkey Jungle, DR
Arenabbottella rosaliae (Pfeiffer, 1858)	MT119711/ NA/ NA	GTW 16507a	Sosúa, DR
Arenabbottella sosuaensis (Bartsch, 1946)	MT119698/ MT119721/ MT119731	GTW 13728c	Cabarete, DR
Arenabbottella sosuaensis (Bartsch, 1946)	MT119699/ NA/ NA	GTW 13728f	Sosúa, DR
Adamsiella ignilabris (Adams, 1849)	MT119687/ NA/ NA	GTW 7244g	Windsor Cave, Jamaica
Annularia anomala (Adams, 1850)	JQ964718/ JQ990572/ NA	ANSP:JBS263-01	Manchester Parish, Jamaica
Annularia chittyi (Adams, 1849)	JQ964706/ JQ990560/ NA	USDA:97J25-01	St. Elizabeth Parish, Jamaica
Annularia fimbriatula (Sowerby, 1825)	JQ964705/ JQ990559/ NA	ANSP:JBS148-01	St. Elizabeth Parish, Jamaica
Annularia fimbriatula (Sowerby, 1825)	JQ964707/ JQ990561/ NA	USDA:97J1-01	Hanover Parish, Jamaica
Annularia fimbriatula (Sowerby, 1825)	JQ964708/ JQ990562/ NA	ANSP:JBS378-01	St. Ann Parish, Jamacica
Annularia hilliana hilliana (Adams, 1845)	JQ964709/ JQ990563/ NA	ANSP:JBS253A-01	Clarendon Parish, Jamaica
Annularia hilliana leporilabre (Adams, 1851)	JQ964710/ JQ990564/ NA	ANSP:JBS133-01	Manchester Parish, Jamaica
Annularia lima (Adams, 1845)	JQ964711/ JQ990565/ NA	ANSP:JBS1-01	St. Elizabeth Parish, Jamaica
Annularia lincina (Linnaeus, 1758)	JQ964712/ JQ990566/ NA	ANSP:JBS398-01	St. Catyherine Parish, Jamaica
Annularia lincinella (Lamarck, 1822)	MT119690/ NA/ NA	GTW 9209d	Rio Cobre, Jamaica
Annularia mitus (Pfeiffer, 1852)	JQ964713/ JQ990567/ NA	ANSP:JBS99-01	St. Catyherine Parish, Jamaica
Annularia pisum (Adams, 1849)	JQ964714/ JQ990568/ NA	ANSP:JBS188-02	Portland Parish, Jamaica
Annularia scabricula (Sowerby, 1843)	JQ964716/ JQ990570/ NA	ANSP:JBS595-01	St. Elizabeth Parish, Jamaica
Annularia triplopoma (Baker, 1934)	JQ964717/ JQ990571/ NA	ANSP:JBS69B-01	Trelawny Parish, Jamaica
Annularisca hendersoni (Torre and Bartsch, 1941)	JQ964763/ JQ990616/ NA	ANSP:CO35B-01	Holguin, Cuba
Annularisca victoris (Torre and Bartsch, 1941)	MT119683/ NA/ NA	GTW 7163e	Playa El Baga, Cuba
Annularisca victoris (Torre and Bartsch, 1941)	KX496697/ NA/ NA	GTW 7163e	Playa El Baga, Cuba
Chondropoma laetum (Poey, 1857)	KX496694/ NA/ NA	GTW 15040a	Velasco, Cuba
Chondropoma oculeum (Watters and Duffy, 2010)	MT119684/ NA/ NA	GTW 7166d	Pedernales, DR
Chondropoma pupiforme (Sowerby, 1843)	KX496717/ NA/ NA	UF 48724	Anguilla
Chondropoma sp.	KX496702/ NA/ NA	GTW 15050a	Rafael Freyre, Cuba
Chondropoma sp.	KX496704/ NA/ NA	GTW 15046a	Guardalavaca, Cuba
Chondropomella magnifica (Pfeiffer, 1852)	KX863609/ NA/ NA	OSUM 42368	Puerto Escondido, DR
Chondropomella magnifica (Pfeiffer, 1852)	KX863610/ KX863590/ NA	OSUM 42358	Bartolomé, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863598/ KX863577/ NA	OSUM 42362	Bombita, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863599/ KX863578/ NA	OSUM 42363	Bombita, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863600/ KX863579/ NA	OSUM 42378	Bartolomé, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863601/ NA/ NA	OSUM 42361	Galindo Adrento, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863602/ KX863581/ NA	OSUM 42377	El Limón, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863611/ KX863591/ NA	OSUM 42359	Bartolomé, DR

(*Continued*)

Appendix 1. (Continued)

Appendix 1

Taxon	GenBank (COI/ 12S/ H3)	Source Accession	Locale
Chondropomium weinlandi (Pfeiffer, 1862)	KX863613/ KX863593/ NA	OSUM 42379	Bartolomé, DR
Chondropomium weinlandi (Pfeiffer, 1862)	KX863618/ KX863597/ NA	OSUM 42364	Bombita, DR
Clydonopoma bartschi (Watters, 2012)	MT119703/ NA/ NA	GTW 14630e	Hispaniolan Pine Biome, DR
Clydonopoma nobile (Pfeiffer, 1852)	KX496730/ NA/ NA	GTW 7089b	Virgen de San Rafael, DR
Clydonopoma nobile (Pfeiffer, 1852)	KX863603/ KX863582/ NA	OSUM 42366	Virgen de San Rafael, DR
Clydonopoma poloense (Bartsch, 1946)	KX863604/ KX863583/ NA	OSUM 42372	Carbon de Polla, DR
Clydonopoma pumilum (Watters and Duffy, 2010)	KX496677/ NA/ NA	GTW 7172b	Las Mercedes, DR
Colobostylus retrorsa (Adams, 1850)	MT119704/ NA/ MT119744	GTW 15700a	Ivy Store, Jamaica
Colobostylus retrorsa (Adams, 1850)	JQ964715/ JQ990569/ NA	ANSP:JBS147-01	Clarendon Parish, Jamaica
Crossepoma marmoreum (Watters and Duffy, 2010)	MT119686/ NA/ NA	GTW 7170i	Cabo Rojo, DR
Crossepoma vermiculatum domingoense (Bartsch, 1946)	KX863614/ NA/ NA	OSUM 42380	Oviedo, DR
Crossepoma vermiculatum domingoense (Bartsch, 1946)	KX863605/ KX863584/ NA	OSUM 42373	Carbon de Polla, DR
Crossepoma vermiculatum domingoense (Bartsch, 1946)	KX863606/ KX863585/ NA	OSUM 42367	Río Palomino, DR
Crossepoma vermiculatum domingoense (Bartsch, 1946)	KX863607/ NA/ NA	OSUM 42374	Cabral, DR
Crossepoma vermiculatum domingoense (Bartsch, 1946)	KX863608/ NA/ NA	OSUM 42376	El Limón, DR
Crossepoma vermiculatum vermiculatum (Bartsch, 1946)	MT119682/ NA/ MT119735	GTW 7088b	Oviedo, DR
Diplopoma crenulatum (Poteiz and Michaud, 1838)	MT119680/ NA/ NA	GTW 7064d	Antigua
Lagopoma lagopoma (Bartsch, 1946)	MT119694/ MT119725/ NA	GTW 10081b	El Valle, DR
Leiabbottella galaxius Watters, 2010	MT119700/ NA/ MT119732	GTW 13813b	Caro Clara, DR
Preclaripoma thompsoni (Watters, 2013)	MT119708/ NA/ NA	GTW 16493e	Majugual, DR
Meganiphe rhecta Thompson, 1978	MT119697/ MT119720/ MT119729	GTW 11371b	Loma del Puerto, DR
Opisthosiphon bahamensis (Pfeiffer, 1865)	MT119688/ MT119727/ MT119738	GTW 8707e	Great Exuma, Bahamas
Opisthosiphon caguanense (Torre and Bartsch, 1941)	MT119715/ MT119728/ NA	GTW 16595a	Cayo Coco, Cuba
Parachondria clenchi (Bartsch, 1946)	MT119714/ NA/ MT119748	GTW 16518b	Talanquera, DR
Parachondria canescens (Pfeiffer, 1852)	MT119678/NA/NA	GTW 179e	Holguin, Cuba
Parachondria dentatus (Say, 1825)	MT119689/ NA/ MT119746	GTW 8709f	Key West, USA
Parachondria gettlemani (Watters, 2012)	MT119702/ NA/ MT119737	GTW 14626b	Virgen de San Raphael, DR
Parachondria pilsbryi (bartsch, 1946)	MT119710/ NA/ MT119750	GTW 16505b	La Isabella, DR
Parachondria trachyderma (Pilsbry, 1933)	MT119709/ NA/ MT119747	GTW 16495f	Cabrera, DR
Pomatias elegans (Müller, 1774)	JQ964789/ JQ990643/ NA	USDA_07FRA03-01	Aquitaine, France
Pomatias elegans (Müller, 1774)	KX496707/ NA/ NA	OSUM 43254	Őrtilos, Hungary
Rolleia oberi Watters and Duffy, 2010	MT119701/ NA/ NA	GTW 14180b	La Cumbre, DR
Superipoma asymmetricum (Pilsbry, 1933)	KX863615/ NA/ NA	OSUM 42369	Puerto Escondido, DR
Superbipoma superbum (Henderson and Simpson, 1902)	KX86361/ KX863592/ NA	OSUM 42360	Bartolomé, DR
Tessaripoma alyshae (Watters and Duffy, 2010)	MT119685/ NA/ NA	GTW 7169c	Puerto Alejandro, DR
Tudorella ferruginea (Lamarck, 1822)	JQ964788.1/ JQ990642/ NA	USDA:Iber99A-01	Balearic Islands, Spain
Tudorella sulcata (Draparnaud, 1805)	GQ370447/ NA/ NA	RES1,2,3	Resquiadou, France
Tudorella sulcata (Draparnaud, 1805)	GQ370448/ NA/ NA	ROU1,2,3	Roucas-Blanc,France
Xenopoma spinososimum Torre and Bartsch, 1941	MT119693/ NA/ NA	GTW 9436d	Cueto, Cuba

Editor's Note

G. Thomas Watters, February 28, 1953–October 10, 2019

The previous article, headed by G. Thomas Watters of the Museum of Biological Diversity at Ohio State University, had been reviewed and was being revised when Tom was diagnosed with cancer in June 2019. Tom left us in October 2019, after fighting the malignancy for four months. Co-authors Megan L. Smith and David J. Sneddon carefully completed the revision and sent the final copy for publication earlier this year.

Tom was a Consulting Editor for *The Nautilus*, wrote frequently in the journal, and was a strong supporter of the journal's publisher, the Bailey-Matthews National Shell Museum, since its inception. In a recent conversation about Tom with citizen scientist and common friend Harry G. Lee, he offered that Tom was a multidisciplinary malacologist in the best tradition of American workers such as Dall, Gould, Pilsbry, and Clench, who were equally proficient and productive working with marine, freshwater, and terrestrial mollusks. Tom will be sorely missed as a husband, father, scientist and professor at his *alma mater*, Ohio State University. I will also miss him as a personal friend and an advocate for this journal.

José H. Leal, Editor
The Nautilus
Bailey-Matthews National Shell Museum

Figure 1. G. Thomas Watters at work as an R. Tucker Abbott Visiting Curator in the Bailey-Matthews National Shell Museum collection, in 2008. Photo by José H. Leal.

Cittarium pica (Linnaeus, 1758) (Gastropoda: Trochoidea: Tegulidae) in southeastern Florida

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ABSTRACT

Fossil and subfossil specimens of the West Indian Top Shell, *Cittarium pica* (Linnaeus, 1758) are found in the Pleistocene rocks and Holocene Native American middens in southeastern Florida. The occurrence of both living and fossil *C. pica* corresponds to hard substrate, represented by rocks exposed both above and below the water level. Pleistocene specimens are found in the Miami Limestone in Miami-Dade County and, for the first time, in the Anastasia Formation in Martin County. In both localities, *C. pica* are found in the vicinity of Pleistocene rocky shorelines. The same pattern is found for Holocene occurrences from archeological digs. Absence of *C. pica* in southern Florida today is likely related to the elimination of suitable habitats during the Holocene marine transgression.

Additional Keywords: Rocky habitats, Pleistocene, Holocene transgression, southern Florida

INTRODUCTION

The trochoidean gastropod, *Cittarium pica* (Linnaeus, 1758), also known as the West Indian Top Snail, currently prospers in multiple tropical and subtropical areas of the western Atlantic: Mexico, Costa Rica, Panamá, Colombia, Venezuela, Bahamas, Cuba, Cayman Islands, Jamaica, Bermuda, Haiti, and Dominican Republic. The northern limits of the species distribution in the western Atlantic are considered to be Bermuda, northern Bahamas (Abacos and Bimini), and the Florida Keys. The larvae of *C. pica* are lecitotrophic, with a life span of 3 to 14 days (Bell, 1992; Hadfield, et al., 1997). From a dispersal standpoint, the larvae survive long enough to reach Bermuda from the northern Bahamas (Robertson, 2003; Olson and Hearty, 2013). The population of *C. pica* in Bermuda had suffered periodic extinctions during historical times. These have been attributed to human over-collecting. The animal's flesh is widely used for food throughout the West Indies (Olson and Hearty, 2013). Artificial reintroductions have been performed several times with very limited success, and harvesting of the species is now illegal in Bermuda (Robertson, 2003). Whereas over-collecting might have played a significant role in eliminating or severely limiting the *C. pica* population in Bermuda, Olson and Hearty (2013) suggested temperature as the primary natural limiting factor for that northernmost recorded marginal habitat of *C. pica* in the western Atlantic during the Holocene and Pleistocene.

While common in the Bahamas today, this species is nearly absent along the southeastern Florida coast (Martin, Palm Beach, and Dade counties), at the same geographical latitude (Figure 1). It is regarded as "rarely" occurring, or having a "dynamic population" in the Florida Keys (Monroe County), and has occasionally even been designated as "locally extinct" in Florida (Abbott, 1974; Robertson, 2003; Olson and Hearty, 2013). Several reintroductions of *C. pica* to the Florida Keys from the Bahamas have been attempted between the years 1930 and 1960, presumably from Cay Sal Bank, Bahamas, with limited degrees of success (Clench and Abbott, 1943; Clench, 1961; Abbott, 1976; Edwards, 1982). Stephenson and Stephenson (1950) did not mention *C. pica* in their study of the Florida Keys intertidal ecology. Voss and Voss (1960) suggested that all specimens found in the Florida Keys were accidentally brought from the Bahamas and Cuba by fisherman, and suggested the absence of "proper habitats" for the species in the Florida Keys.

All published observations on the ecology of *C. pica*, clearly suggest that the occurrence, survival, and successful reproduction of the species in the western Atlantic is strongly dependent on the presence of rocky intertidal habitats. These habitats can be comprised of rock of any origin, but must have abundant exposed surfaces both below and above sea level. It also appears that the rocky habitat, protected or unprotected, must be facing the "open sea" (Herrera et al., 2012; Debrot, 1990; Bandel and Wedler, 1987; Vermeij, 1972, 1973; Randall, 1964; Robertson, 2003; Houbrick, 1968; Redfern, 2001; Humfrey,1975; Urosa,1972). The reference to the "open sea" is likely related to an additional limiting factor for the successful

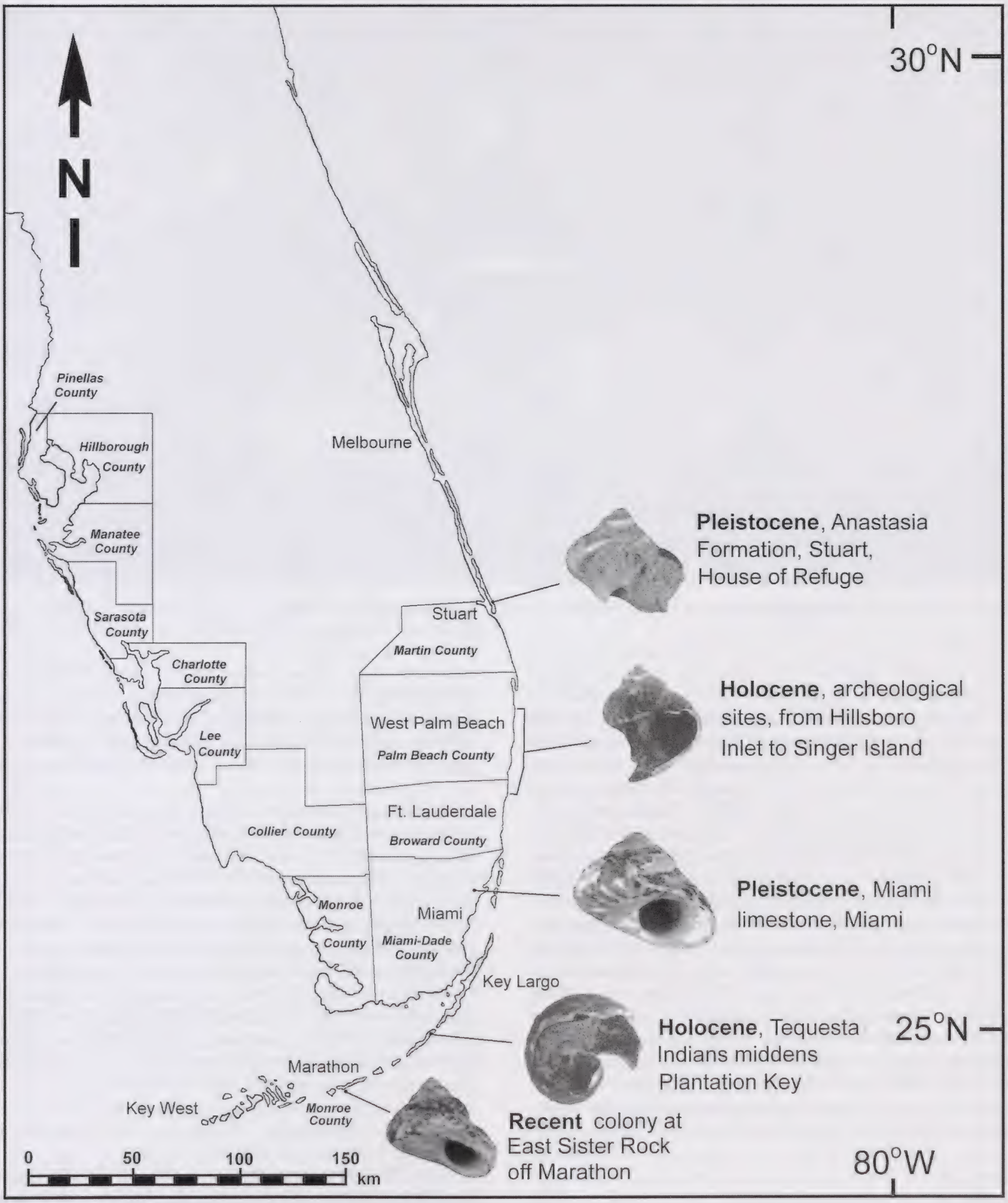


Figure 1. Occurrence of *Cittarium pica* in Florida (Pleistocene through Recent).

survival of *C. pica* populations mentioned in the literature—a low tolerance of the species to freshwater intrusions. Such a pattern is documented along northern Colombia where there are dwindling populations of otherwise abundant *C. pica*. Studied areas in Colombia were not subjected to extreme harvesting, and have the necessary rocky intertidal habitats for this species to survive. However, low salinity in these regions was

correlated with the animal's failure to thrive (Herrera et al., 2012). Freshwater input such as river flow will most likely negatively affect any *C. pica* habitat. Low salinity can, potentially, be a localized limiting factor, which would be more important next to large landmasses with river discharge. The Florida Peninsula is a large landmass compared to most Caribbean Islands. However, lack of suitable habitats makes it difficult to assess the importance of reduced salinity as a factor limiting *C. pica* populations in Florida.

As with the majority of marine gastropods, the size distribution of *Cittarium pica* increases with distance from the shoreline. Juveniles are known to flourish closer to the shore, in the intertidal zone, while mature *C. pica* are able to survive in subtidal areas (Humfrey,1975; Robertson, 2003). Juvenile *C. pica* are particularly dependent on rocky surfaces within the intertidal zones, attaching themselves to rock surfaces during their most vulnerable developmental stages (Urosa,1972). *Cittarium pica* reach sexual maturity at a shell length (diameter) of 32–34 mm. Adult *C. pica* grow much larger shells, often exceeding 100 mm (Robertson, 2003). It has also been noted that specimens of *C. pica* living in wave-exposed habitats have a smaller average shell size, and reach maturity at smaller shell sizes, than in sheltered habitats. This has been attributed to lower rates of survival and growth, mainly due to higher activity of shell-drilling and crushing predators in open habitats exposed to wave action (Debrot, 1990).

Fossils of *C. pica* in the western Atlantic are known from rocks no older than the Pleistocene. A well-documented Pleistocene record of *C. pica* in Bermuda goes back to the Marine Isotope Stage (MIS) 11, approximately 400,000 ybp (Epstein and Lowenstam, 1953; Richards et al, 1969; Olson and Hearty, 2013). In Jamaica, *C. pica* is recorded from the late Pleistocene, Last Interglacial (Donovan and Littlewood, 1993), presumably MIS 5. Pleistocene occurrences in southeastern Florida were cited as "quite common" by Abbott and Morris (1995). However, the only published record that provides details on locality is the occurrence in the Miami Limestone mentioned by Halley and Evans (1983). The presence of fossils in "subrecent", probably Holocene deposits, was noted for Cuba, Aruba, Curaçao, and Barbados (Weisbord, 1962). Numerous shells of the *C. pica* were found in the southeastern Florida and Florida Keys in the late Holocene Tequesta (Native American tribe) middens, (Goggin, 1944; Wheeler et al, 2002) (Figure 1). The focus of this paper is to examine Pleistocene through Recent occurrences of *C. pica* in southeastern Florida, with reference to its habitat, in order to evaluate factors potentially controlling the occurrence and distribution of the species in south Florida.

MATERIALS AND METHODS

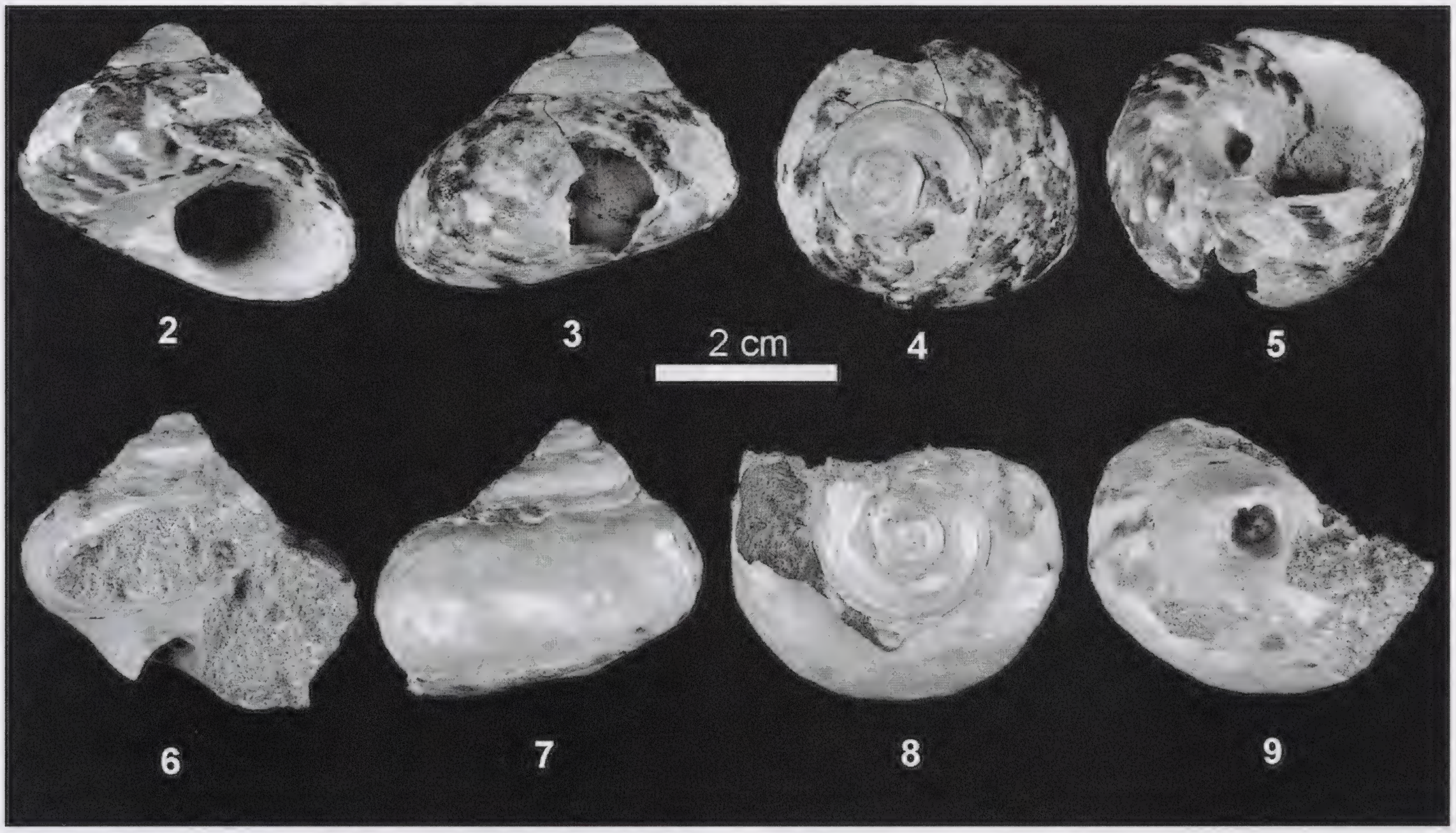
Four complete (UF 307072–UF 307074, UF 317477) and three fragmented specimens of *C. pica* were collected from an outcrop of Miami Limestone at the intersection of First Avenue (Kagoshima Boulevard) and 13th Street (Coral Way), in Coral Gables, Florida (25°45.733' N, 80°11.716' W) by the senior author. The outcrop is about 5.5 m above the present sea level, with an exposed thickness of approximately 3 m. A shell lag deposit of smaller mollusks co-occurs with larger shells of *C. pica*. Halley and Evans (1983) listed bryozoan fragments, a small bivalve *Donax* sp., as well as several fossilized corals (*Porites sp., Siderastrea sp.* and *Montastraea cavernosa*) at this outcrop (Figure 1). A single specimen of *C. pica* (UF 307071) was collected by the senior author at the base of the 3.5 m high beach cliff of the Anastasia formation in Stewart, Martin County (27°12′00.59″ N, 80°09′56.05″ W). The locality is known as the "House of Refuge" (Lovejoy, 1998) (Figure 1). At this location, the rock is a tan-colored, sandy, and a poorly sorted planar-bedded coquina with granular texture and abundant shell hash. Shells of *C. pica* are easily identifiable by their shape, and preserved characteristic black and white color pattern. All collected shells had broken apertures, and were abraded to various degrees (Figures 2–9), indicating reworking in a nearshore zone.

All fossil specimens illustrated in this article (Figures 2–9) are deposited in the Florida Museum at the University of Florida in Gainesville (UF). During the summers of 2018 and 2019 the senior author conducted a number of boat-based surveys of all the localities in the Florida Keys where living *C. pica* had been collected between 1973 and 1975 (Abbott, 1976). These localities were: yacht basin at Marathon (24°42′12.42″ N; 81°05′39.17″ W), East Sister Rock off Marathon (24°41′12.93″ N; 81°04′28.37″ W), Molasses Keys (24°41′08.67″ N; 81°11′17.34″ W), and the ocean side of the Ohio-Missouri Keys channel (24°40′32.64″ N; 81°14′20.79″ W). The surveys recorded the presence or absence of live *C. pica* and/or dead shells, the type of habitat/substrate, the water temperature at the time of collecting, depth of occurrence, the size of observed individuals, and their approximate number.

Museum collections worldwide were searched for the fossil and recent records of *C. pica* in Florida. Institutional acronyms used are: UF: Florida Museum of Natural History, Gainesville; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC; OPM: Okinawa Prefectural & Art Museum, Okinawa, Japan; OMNH: Osaka Museum of Natural History, Osaka, Japan; CM: Carnegie Museum of Natural History, Pittsburgh; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge; ZMB Moll: Museum für Naturkunde, Berlin, Germany; RMNH.MO & ZMA. MOL: Naturalis Biodiversity Center, Leiden, Netherlands.

GEOLOGIC SETTING

The late Pleistocene formations of southern Florida, Miami Limestone, Anastasia Formation, and upper part of the Key Largo Limestone were deposited during the Sangamonian interglacial period, also referred to as Marine Isotope Stage 5e (MIS 5e) dated at approximately 125,000 ybp. In southern Florida, within this timeframe, sea level was estimated to be approximately 6.7 m above that of today (Hickey et al., 2010). This warm period lasted approximately 10 ka (Shackleton,



Figures 2–5. *Cittarium pica*, UF307072, Pleistocene, Sangamonian, Miami Limestone, Miami. **Figures 6–9.** *Cittarium pica*, UF307071, Pleistocene, Sangamonian, Anastasia Formation, Stuart.

1969). Uranium-series dating (Th^{230}/U^{234}) of oolite samples from the Miami Limestone yielded ages of approximately 130,000 ybp. These results are contemporaneous with the uppermost part of the Key Largo Limestone (Osmond et al, 1965; Broeker & Thurber, 1965).

The Miami Limestone (Sanford, 1909) has been subdivided into three distinct facies: the bryozoan facies, the mottled facies and the bedded facies. Of these three, the mottled and the bedded facies are confined to the topographic high of the Atlantic Coastal Ridge, where they are exposed in a vertical succession (Evans, 1982). Shells of *C. pica* were found in one of the outcrops of the bedded facies. The locality and the facies were described as the "islands on the shoals", and the occurrence of *C. pica* was recorded by Halley and Evans (1983). The locality consists of a layer of carbonate conglomerate on top of an erosional surface, and overlain by low-angle seaward-dipping beds. The low dip angles (5–18°) of these beds are indicative of a low-angle beach berm. The conglomerate deposits contain fragments of reworked corals: *Porites* sp., *Siderastrea* sp., and *Montastrea* sp., as well as cemented fragments of the cross-bedded Miami Limestone. This indicates that these pieces were already cemented and were incorporated into a beach or nearshore deposit in a fully cemented state. These facies of the Miami Limestone are interpreted as deposited at or near the shoreline, in the proximity of islands composed of cemented oolitic limestone (Halley and Evans, 1983).

The Anastasia Formation (Sellards, 1912) is considered to be the youngest lithified deposit along Florida's southeastern coast (Perkins, 1977; Petuch, 2007). It consists of interbedded quartz sand, and coquina limestone, cemented by quartz and calcite cement. There are also whole and fragmented remains of mollusks, poriferans, bryozoans, arthropods, echinoderms, and some vertebrate remains (Scott, 1991; DuBar, 1974; Portell et al., 2003). Both U^{234}/Th^{230} dating (Osmond et al., 1970) and amino-acid racemization dating of contained bivalve fragments (Mitterer,1974) yielded a date of deposition of approximately 110,000 ybp. It should be noted that younger radiocarbon dates (8500–9000 ybp) for the Anastasia Formation were obtained from Anastasia Island in northeastern Florida (Murphy, 1973). It is therefore possible that parts of the Anastasia Formation, especially to the north, are diachronous to the Anastasia Formation rocks in the south. The Anastasia Formation is exposed along the coastline of Florida from St. Augustine in the north, to Boca Raton in the south (Scott, 1991; Lovejoy, 1998). It is also widely exposed underwater, at depths of 3–7 m in Broward and Palm Beach counties. The Anastasia Formation in Martin and Palm Beach counties forms the foundation of the Atlantic Coastal Ridge. South of Palm Beach County, it grades into the oolitic Miami Limestone. Thickness of the Anastasia Formation varies from 5.5 m of surface exposure in Palm Beach County, to 37.8 m in a subsurface section in Brevard County (Parker et. al, 1955; DuBar, 1974). The depositional environment of the Anastasia Formation in coastal outcrops is traditionally interpreted as a high-energy offshore sand bar,

which was later cemented and exposed as beachrock (DuBar, 1974; McNeill, 1985; Lovejoy, 1987).

RESULTS

Pleistocene specimens of *C. pica* from southern Florida (Figures 2–9) were only found at locations where geologic evidence indicates the existence of a hard rock substrate or exposure, at or near the site of collection. Specimens from the Miami Limestone attain a size of up to 60 mm in diameter and 58 mm in height, suggesting that they represented adults or young adults. No museum records of Pleistocene or older specimens of *C. pica* were located. Specimens collected from the Pleistocene in Bermuda are stored at the Yale Peabody Museum, Invertebrate Paleontology Division. *Cittarium pica* in the Miami Limestone co-occur with *Diodora listeri*, both diagnostic of hard rocky substrates. Halley and Harris (1979) concluded that the rocky islands, made from cemented oolite, had formed late in the depositional history of the Miami Limestone before the sea-level fall during MIS2. Alternatively, the islands could have been exposed above the sea level, as a result of minor sea-level fall during MIS 5. Formation of hard substrates composed of lithified skeletal sand along the coastal zone could have occurred simultaneously to the north, in Palm Beach County, as a result of similar processes, forming the coquinoid limestone of the Anastasia Formation (Figure 14). The specimen of *C. pica* found *in situ* in the coquinoid limestone of the Anastasia Formation in Martin County supports that conclusion. It is also the northernmost Pleistocene specimen of *C. pica* found in southeastern Florida.

A survey in the summers of 2018–2019 of the localities in the Florida Keys reported to have living populations of *C. pica* by Abbott (1976) revealed that only one such population still persists, the one along the western side of East Sister Rock off Marathon, (24°41′12.82″ N; 81°04′29.22″ W) (Figure 1). The majority of the observed specimens, both living and dead, were 9–10 cm in diameter, but one small, juvenile specimen (3 cm in diameter) was found dead. The presence of multiple living adult specimens in July of 2019, suggests the existence of a breeding population at this locality. All live specimens found at East Sister Rock were observed at a depth of 1–2 m, on broad underwater rock exposures of the Key Largo Limestone along the western side of East Sister Rock (Figures 10, 11). At least some of these rocks could have been artificially placed there to enhance shoreline protection.

Very fresh, dead shells of *Cittarium pica* were also recorded in the Dry Tortugas, in the vicinity of Fort Jefferson (Figures 12, 13). Shells of *C. pica* were carried by land hermit crabs, *Coenobita clypeatus* (Fabricius, 1787) just as happens in Bermuda. Museum records contain shells of *C. pica* from Dry Tortugas, particularly from the Bush Key, that were collected from Native American middens (UF 9588, 9591–9598). Although live *C. pica* were not observed in the Dry Tortugas, the freshness of shells carried by *C. clypeatus* suggest the likelihood of a live *C. pica* colony in that area.

DISCUSSION

Temporal patterns of extinction and recolonization of *C. pica* in Bermuda (32° N) during the Quaternary clearly indicate that temperature was a main factor determining survival of this species at the northernmost extent of its range.

This trend corresponds well to climate changes during the glacial-interglacial stages. Cold sea-surface temperatures during the glacial periods, and the onset of cold sea-surface temperatures (SST) after MIS 5e made Bermuda uninhabitable for *C. pica*. The appearance of *C. pica* during the warmer interglacial (MIS 11, 9, 5, and 1) clearly demonstrates the dependence of this species on warm tropical waters. It was also noted that lowering of sea level during glacial stages (MIS 12, 10, 8, 6, and 2) helped to form extensive, exposed rocky surfaces at sea level, resulting in creation of an ideal habitat for *C. pica* (Olson and Hearty, 2013). *Cittarium pica* re-appeared in Bermuda in the 17th and 18th centuries (MIS1), only to be apparently exterminated by humans for food (Clench and Abbott, 1943; Robertson, 2003; Olson and Hearty, 2013).

Low winter water temperatures are not likely to be a contributing factor to the near absence of *C. pica* in southeastern Florida today. This species inhabits areas at the same latitude and with similar temperature ranges in the Bahamas. The sea surface temperatures range from 23.1°C (January) to 30.8°C (August) for West End, Grand Bahama Island, Bahamas, and from 23°C (January) to 30°C (August) in Key West, Florida (World Sea Temperatures, 2019). This is similar to a temperature tolerance range of the *C. pica* throughout the western Atlantic. The average monthly sea temperatures recorded in Lameshur Bay, St. John, during the *C. pica* growth period (Summer) ranged from 26.7 to 29.9°C (Randall, 1964). Winter temperatures can occasionally fall to 19°C in parts of southern Florida, but not for extended periods of time.

Coastal areas off Miami-Dade, Palm Beach and Martin Counties are also not affected by summer upwelling in the Straits of Florida (Taylor and Stewart, 1959; Smith, 1981; Pitts and Smith, 1992). The presence of a living colony of *C. pica* on hard rock substrate at East Sister Rock, off Marathon also suggests that the low winter temperatures in southern Florida are most likely not an obstacle for the successful survival of this species. The major difference between southeastern Florida and the western Bahamas is not in sea surface temperature but in the presence of abundant exposed and shallow submerged rocky habitats in the Bahamas that are absent in Florida. Today, *C. pica* commonly occur in Bimini, Bahamas at 25° N (the same latitude as Miami, Florida), and up to 27° N, in Abaco, Bahamas. All occurrences in the Bahamas are on intertidal to subtidal exposed rocks, a preferred habitat of this species (Abbott, 1974). Abbott (1976) and Edwards (1983) had commented on several living populations of

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11

12

13

Figures 10–11. Live *Cittarium pica* (Linnaeus,1758) at the East Sister Rock, off Marathon Florida Keys, photo taken July 2019. **Figures 12–13.** Very freshly dead shells of the *Cittarium pica* in Fort Jefferson, Dry Tortugas, Florida, carried by land hermit crabs *Coenobita clypeatus*. Photo by Scott Oropeza in August 2019, courtesy of Dale Bittner.

C. pica that were either purposefully, or accidentally introduced by man or, possibly, arrived as floating larvae. Edwards (1983), referring to a letter from William J. Clench, stated that live *C. pica* were brought from the Cay Sal Bank, Bahamas, and released at Marathon in the early 1950 by Richard Decker and Al Pflueger. Presumably, the population on East Sister Rock observed by the senior author, had survived since that time. The living *C. pica* population on East Sister Rock in Marathon, although the only one directly observed by the senior author, may not be the only one in existence in Florida. Examination of the museum records, revealed an occurrence pattern that may suggest the presence of live *C. pica* in Florida, north of Florida Keys, on rocky substrates. Apart from outright erroneous museum locality data like "India" (OPM 702791, 702792), "USA Texas" (OMNH KJ29), "Indonesia" (ZMB Moll 92203), "Tanzania, Zanzibar" (ZMA.MOLL.99822), "Chile" (CM #62.23049), and one confirmed erroneous record from Saint Petersburg, Florida (RMNH.MOL. 296543, Steven van der Mije, pers. comm, Nov. 2019), all records from Florida fall into two broad categories. In the first category are shells collected from Native American middens. The majority of these were collected in Dry Tortugas (Bush Key) and some in the southwestern Florida, in Collier (UF 234620) and Sarasota (MCZ 282977) counties. In the second category are fresh and/or live collected shells. Most of these are from the Lower Keys, Monroe County: Big Pine Key (UF 122094), Bahia Honda Key (UF 52197), Sawyers Key (UF 153286), Boca Chica Key (USNM 1410655), Little Duck Key (2008, UF 434273), Monroe County (?), between Cape Sable and Cape Romano (UF 321485. There are also two records in this category that may suggest survival of *C. pica* on the rocky bottom as far north as Jupiter, Palm Beach County (UF 153287), and Pinellas County, NW of Tarpon Springs (UF 9589) in southwestern Florida (Figure 1). The same specimen from Jupiter (UF 153287), collected

in 1946 was considered to be subfossil or fossil. It has been described as "chalky with loss of the dark pigmentation in their shells, which was replaced by a muted brown color" (Clench and Abbott, 1943; Robertson, 2003), yet reported as "unabraded possibly live collected" (John Slapcinsky, pers. comm, Dec 2019). Specimens from Pinellas County (UF9589), on the other hand, look fresh and were collected as a bycatch by sponge fisherman (John Slapcinsky, pers. comm. Dec. 2019). Specimens of *C. pica* sometimes found on the beach throughout Broward and Palm Beach counties were usually interpreted as eroded recent shells, possibly brought from the Bahamas. A specimen of similar preservation was found by the first author of this paper at Pompano Beach in 2018.

The Holocene MIS 1 records of *C. pica* in Florida comes from archeological digs of the Tequesta Natives middens on Plantation Key (24°N), and as far north on the southeastern coast of Florida as Boca Raton and Boynton Beach, at 26°N (Goggin, 1944; Wheeler et al, 2002) (Figure 1). Based on the ceramics, the archeological sites in Boca Raton and Boynton Inlet, have been dated to the Glades I and II periods, ~ 2500–800 ybp (Wheeler et al, 2002). Goggin (1948) noted that *C. pica* occurrences at the archeological sites between Hillsboro Inlet and Singer Island correspond to areas of rocky outcrops along the shoreline, and observed that the abundance of *C. pica* shells in southeastern Florida sites, and their proximity to the rocky shorelines is an indication that shells were collected locally for food, and not obtained by trade from the Florida Keys or the Caribbean.

Sea level fall during the late Pleistocene (MIS 2) had exposed broad areas of Pleistocene shallow shelf, and aided further cementation of Pleistocene bedrock units, including both the Miami Limestone to the south and the Anastasia Formation to the north. The shoreline once again moved seaward. Subsequent Holocene transgression flooded and currently conceals rocks of the age that might contain more fossils of *C. pica.* Alternatively, *C. pica* might have been absent from Florida during MIS2 because of the colder water temperatures during the Last Glacial Maximum.

The Holocene sea-level rise following the Younger Dryas event, however, did not reach levels as high as during the Sangamonian Interglacial (MIS 5). Although an extensive rocky shoreline comprised of coastal cliffs, known today as the Anastasia Formation exists along the southeastern Florida coastline, the cliffs are typically located above the mean high tide and separated from the underwater outcrops of the Anastasia Formation by extensive sand fields. Holocene transgression also brought in a large amount of transgressive sand to the eastern Florida coast (Hine, 2013). The sand washed ashore, created today's southeastern Florida beaches, while simultaneously covering large portions of the Anastasia Formation in areas immediately above and below the tide line. All beaches of southeastern Florida are underlain by Pleistocene bedrock. As the sea-level gradually rose, transgressive sand gradually buried the exposed hard substrates formed by both the Miami Limestone and the Anastasia Formation, gradually splitting and eliminating the remaining habitats of *C. pica* along the

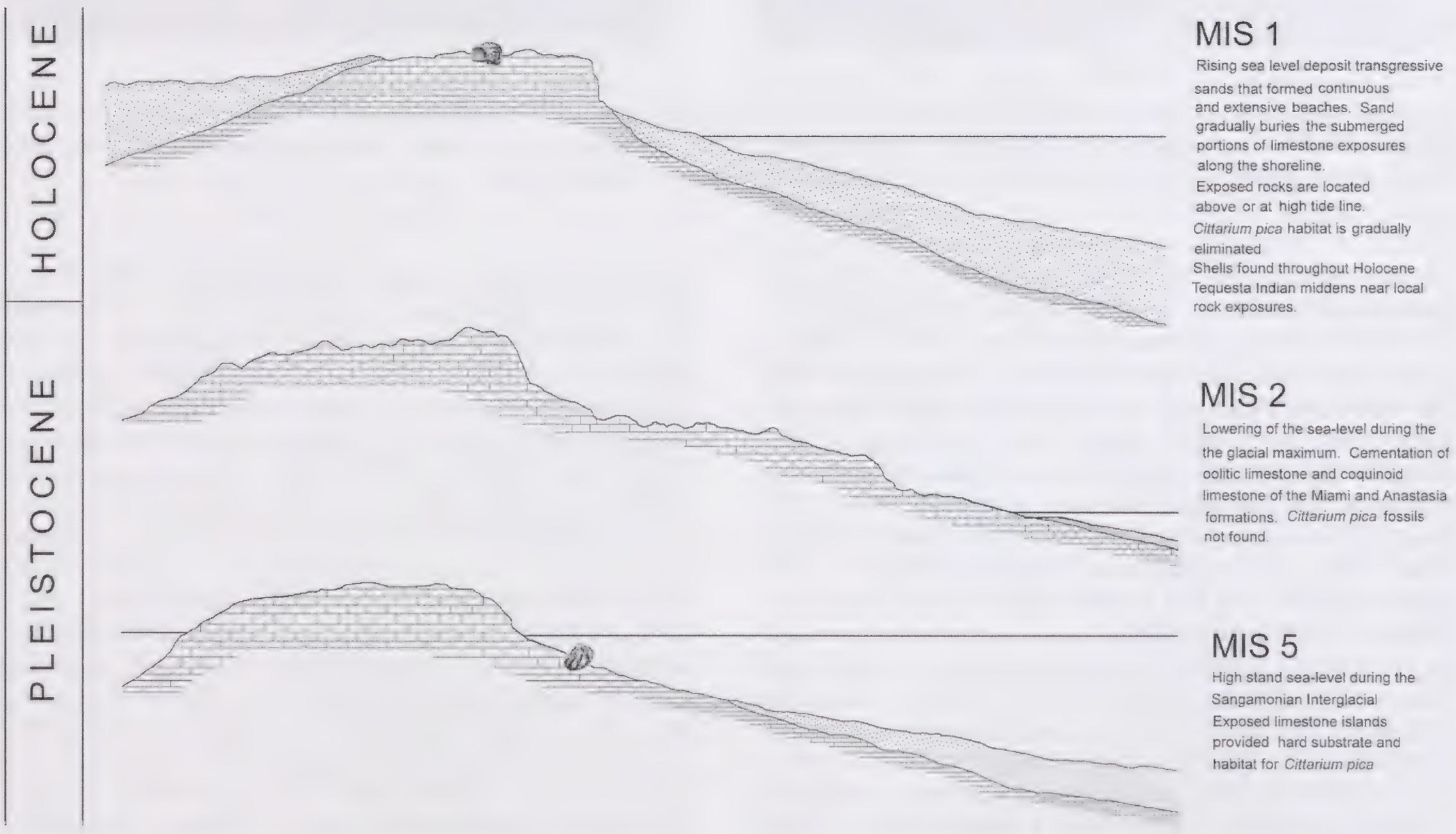
HOLOCENE
PLEISTOCENE
MIS 1
Rising sea level deposit transgressive sands that formed continuous and extensive beaches. Sand gradually buries the submerged portions of limestone exposures along the shoreline.
Exposed rocks are located above or at high tide line.
Cittarium pica habitat is gradually eliminated
Shells found throughout Holocene Tequesta Indian middens near local rock exposures.
MIS 2
Lowering of the sea-level during the the glacial maximum. Cementation of oolitic limestone and coquinoid limestone of the Miami and Anastasia formations. *Cittarium pica* fossils not found.
MIS 5
High stand sea-level during the Sangamonian Interglacial
Exposed limestone islands provided hard substrate and habitat for *Cittarium pica*

Figure 14. Diagram of the Pleistocene and Holocene sea-level changes related to *Cittarium pica* habitats in southern Florida.

southeastern Florida coast. That process continued throughout the Holocene, with dwindling colonies of *C. pica* surviving at suitable rocky habitats until completely buried by sand (Figure 14). The absence of *C. pica* along the southeastern coast of Florida today, therefore, is most likely a result of elimination of suitable habitats by sand burial, during the Holocene transgression.

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Two new species of genus *Bathyacmaea* from deep-sea chemosynthetic areas in the western Pacific (Gastropoda: Pectinodontidae)

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ABSTRACT

Two new species of the genus *Bathyacmaea* Okutani, Tsuchida and Fujikura, 1992 are described and illustrated from deep-sea chemosynthetic areas in the western Pacific. ***Bathyacmaea austrina* new species**, sampled from hydrothermal vents in Okinawa Trough at depths of 1314–1374 m, is closely related to *Bathyacmaea secunda* Okutani, Fujikura, and Sasaki, 1993 in having a rounded shell outline, but differs in having beaded shell sculpture. ***Bathyacmaea brevidentata* new species**, collected from a methane seep area in the South China Sea, is most similar to *Bathyacmaea lactea* Zhang, Zhang, and Zhang, 2016 in having a thick shell with regularly-spaced concentric growth lines, but can be separated from it by having a highly arched shell with a concave aperture margin. Phylogenetic reconstruction based on partial sequences of COI also support their placements within *Bathyacmaea*.

Additional Keywords: Patellogastropoda, chemosynthetic environment, COI

INTRODUCTION

The genus *Bathyacmaea* is a small group of deep-sea limpet that are restricted to chemosynthetic environments in the western Pacific. To date, a total of seven species have been described from various localities (see Table 1). Of them, two species, *Bathyacmaea secunda* Okutani, Fujikura, and Sasaki, 1993 and *Bathyacmaea tertia* Sasaki, Okutani, and Fujikura, 2003 are found in the Okinawa Trough, and one species, *Bathyacmaea lactea* Zhang, Zhang, and Zhang, 2016, is from South China Sea.

Several limpet specimens were collected during an expedition to deep-sea chemosynthetic areas at Okinawa Trough and South China Sea in 2016 by Institute of Oceanology, Chinese Academy of Sciences (IOCAS). Observations of the shell and radula morphology revealed that they represent two undescribed species belonging to the genus *Bathyacmaea* Okutani, Tsuchida, and Fujikura, 1992. In this article, we describe and illustrate these two species as new to science, and compare them to their related congeners.

MATERIALS AND METHODS

The specimens studied were collected during several dives of the ROV Faxian (based on mother ship R/V Kexue). The specimens were then fixed in 99.5% ethanol soon after collection. For study, shells and soft parts were examined under light microscopy, and the radulae by both light and scanning electron microscopy (SEM). For SEM studies, radular sacs were extracted via gross dissection, cleaned using 10% NaOH for 2–3 hours, rinsed in distilled water, air-dried, coated with gold, and examined using scanning electron microscopy. Two specimens of each species were selected for amplification of the partial COI sequences. As a result, two sequences from ***Bathyacmaea brevidentata* new species**, and one sequence from ***Bathyacmaea austrina* new species**, were obtained and have been deposited in GenBank (accession numbers: MK341688, MN180052–MN180053). Sequencing and phylogenetic methods follow that of Zhang and Zhang (2017). Type materials are deposited at the Marine Biological Museum, Chinese Academy of Sciences (MBM CAS), Qingdao, China.

SYSTEMATICS

Family Pectinodontidae Pilsbry, 1891

Genus *Bathyacmaea* Okutani, Tsuchida, and Fujikura, 1992

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Table 1. List of species of *Bathyacmaea* from vent/seep habitats (species arranged in alphabetical order)

Species	Distribution
***Bathyacmaea austrina* new species**	Okinawa Trough, 1314–1374 m, vent
Bathyacmaea becki Zhang and Zhang, 2017	Manus Back-Arc Basin, 1714–1853 m, vent
Bathyacmaea jonassoni Beck, 1996	Edison Seamount, 1483 m, vent
Bathyacmaea lactea Zhang, Zhang, and Zhang, 2016	South China Sea, 1132 m, seep
Bathyacmaea nipponica Okutani, Tsuchida, and Fujikura, 1992	Off Hatsushima, Sagami Bay, 1110–1200 m, seep
Bathyacmaea secunda Okutani, Fujikura, and Sasaki, 1993	Okinawa Trough, 700–1430 m, vent
***Bathyacmaea brevidentata* new species**	South China Sea, 1120 m, seep
Bathyacmaea subnipponica Sasaki, Okutani, and Fujikura, 2003	Nankai Trough, 1100 m, seep
Bathyacmaea tertia Sasaki, Okutani, and Fujikura, 2003	Okinawa Trough, 996–1000 m, vent

Type Species: *Bathyacmaea nipponica* Okutani, Tsuchida, and Fujikura, 1992.

***Bathyacmaea austrina* new species**
(Figures 1–9)

Description: SHELL (Figures 1–5), patelliform, of medium size for genus, up to 16.6 mm long, thick (ca. 0.8 mm above aperture margin in holotype), semitransparent. Outline nearly rounded, longer slightly than wide, width 91–99% (mean 95%) of length. Profile low for genus, height 19–32% (mean 27%) of shell length. Apex slightly anterior to center, moderately eroded, protoconch not preserved. All slopes straight. External surface whitish, sculpture consisting of undulated concentric growth lines, forming prominent beads at intersections with developed axial ribs. Aperture margin convex at sides, slightly reflected.

SOFT PARTS (Figure 9): Animal with tapering tentacles, eyes absent. Head stout and rounded, without oral lappets. Mantle edge smooth, with no papillae. Ctenidium bipectinate and large. Intestine blackish in color. Gonad situated at posterior end of visceral mass. Urogenital papilla digitiform, relatively long, situated right-anteriorly to visceral mass. Pericardium whitish, triangular, situated left-anteriorly to corner of visceral mass.

RADULA (Figures 6–8): Formula 0+1+0+1+0. Rachidian tooth vestigial, represented by a longitudinal, ridge-like structure. Rachidian basal plate wider than long. Lateral tooth ca. 180 μm long, with a straight, stout shaft, tip divided into three cusps. All three cusps outwardly bent, innermost and middle cusps spoon-shaped and subequal in size, outermost one thin, narrow, with an acute tip.

Type Locality: Daiyon Yonaguni Knoll, Okinawa Trough, 24°51′ N 122°42′ E, at 1374 m depth.

Type Material: Holotype: MBM286516, collection number: RY16097, 25 Aug. 2016. **Paratypes 1–5**, MBM 286517, collected together with holotype at type locality. **Paratypes 6–8**, MBM 286518, Izena Hole, Okinawa Trough, 27°16′ N, 127°05′ E, 1314 m, 23 Aug. 2016. For measurements, see Table 2.

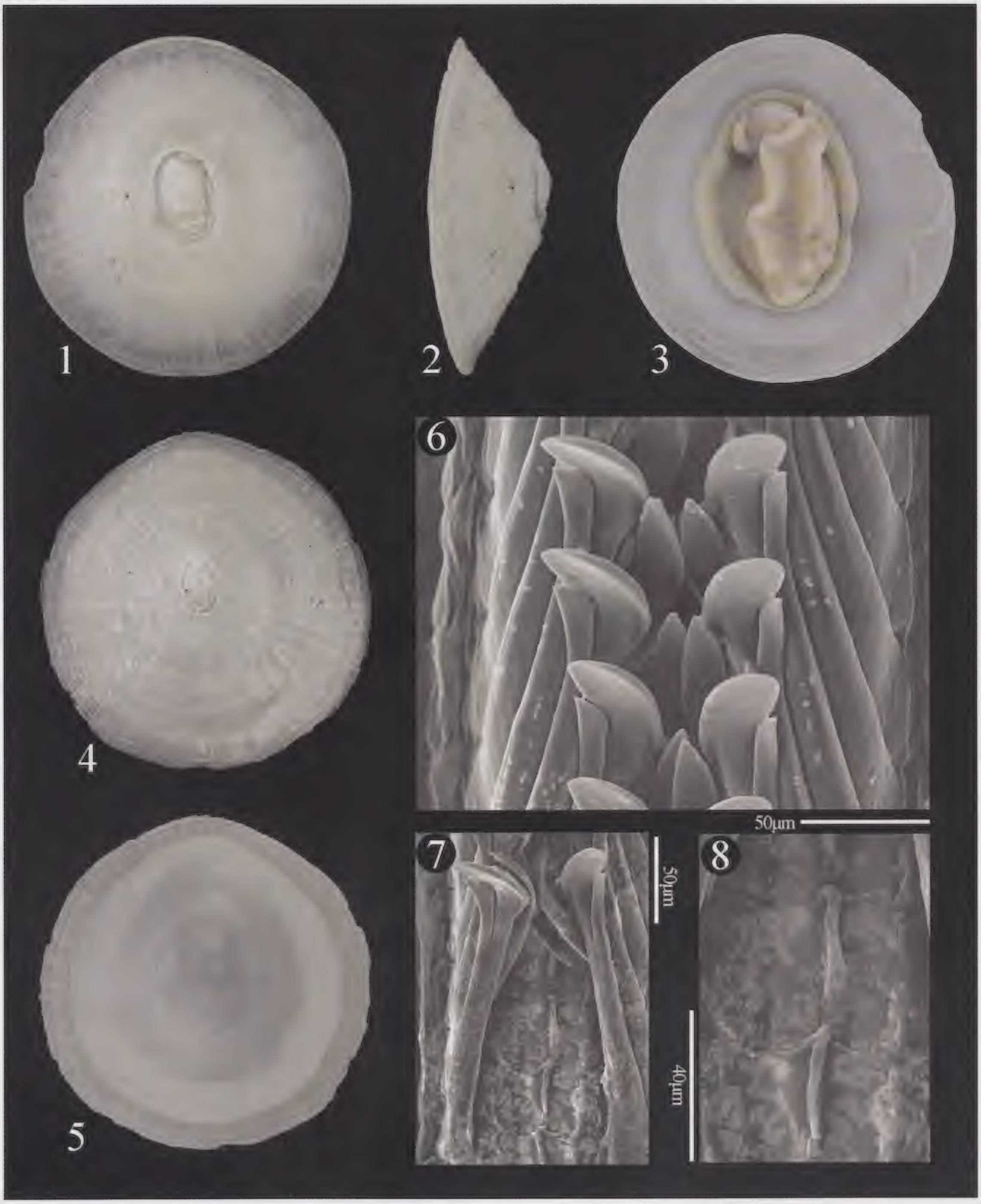
Distribution and Habitat: Okinawa Trough, from two hydrothermal vent sites, Daiyon Yonaguni Knoll and Izena Holesite, 1314–1374 m, attached on black rocks and shells of *Bathymodiolus platifrons* Hashimoto and Okutani, 1994.

Etymology: Latin *austrina*, the southern part of a geographic unit, used in apposition, and referring to the type locality, located in the southernmost part of the Okinawa Trough.

Remarks: *Bathyacmaea austrina* new species was collected from two hydrothermal vent sites, Daiyon Yonaguni Knoll and Izena Hole, both in the Okinawa Trough. At the Izena Hole site, another species of the genus, *Bathyacmaea secunda* Okutani, Fujikura, and Sasaki, 1993, was also sampled, at a depth of 1328 m. The two species are very similar by having a rounded shell outline. However, *Bathyacmaea secunda* has a smoother

Table 2. Shell measurements (in mm) and ratios of ***Bathyacmaea austrina* new species**.

	Length (L)	Height (H)	Width (W)	H/L ratio	W/L ratio
Holotype	16.6	4.5	16.0	0.27	0.96
Paratype 1	12.0	3.8	11.8	0.32	0.98
Paratype 2	14.2	2.7	13.5	0.19	0.95
Paratype 3	12.3	3.8	11.7	0.31	0.95
Paratype 4	16.3	4.0	16.1	0.25	0.99
Paratype 5	11.9	3.3	11.3	0.27	0.95
Paratype 6	11.0	3.5	10.0	0.32	0.91
Paratype 7	11.2	3.2	10.3	0.29	0.92
Paratype 8	10.4	2.0	9.8	0.19	0.94
Average	12.9	3.4	12.3	0.27	0.95



Figures 1–8. ***Bathyacmaea austrina*** **new species**. **1–3. Holotype**, MBM286516, length 16.6 mm. **4–5. Paratype 1**, MBM286517, length 12.0 mm. **6.** Dorsal view of intact radular segment. **7–8.** Rachidian region, showing the single lateral tooth and the vestigial rachidian teeth.

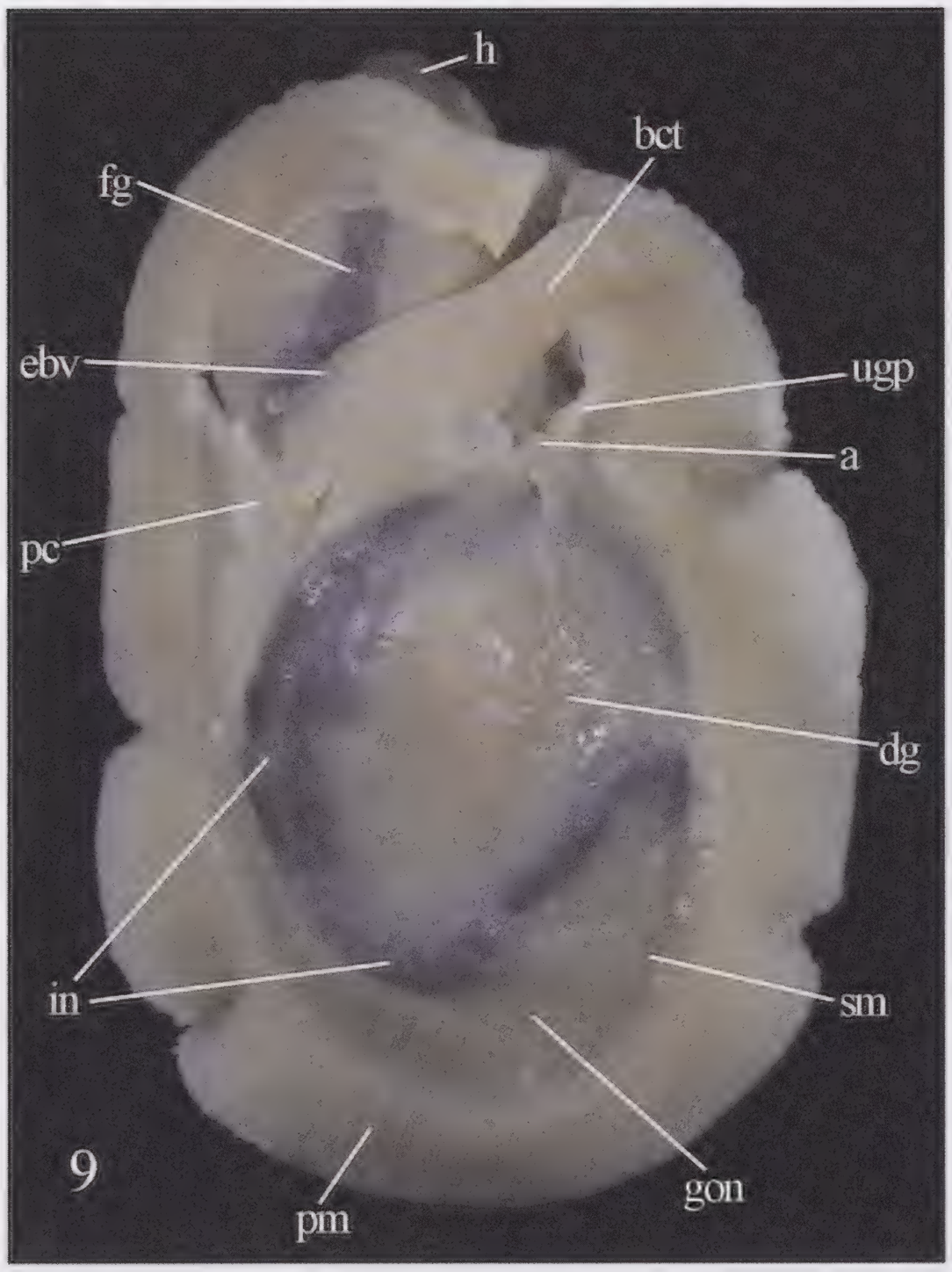


Figure 9. Dorsal view of the soft parts of ***Bathyacmaea austrina* new species**, 5 mm. Abbreviations: **a:** anus; **bct:** bipectinate ctenidium; **dg:** digest gland; **ebv:** efferent branchial vein; **fg:** fore gut; **gon:** gonad; **h:** head; **in:** intestine; **pc:** pericardium; **pm:** pallial margin; **sm:** shell muscle; **ugp:** urogenital papilla.

sculpture, and the outermost cusp of lateral tooth is remarkable broad with a truncated tip. Although *Bathyacmaea nipponica* Okutani, Tsuchida, and Fujikura, 1992 and *Bathyacmaea subnipponica* Sasaki, Okutani, and Fujikura, 2003 both have beaded shell sculptures, their oval shell with high profile, and distinctive radular features can readily separate them from ***Bathyacmaea austrina* new species**.

Bathyacmaea brevidentata new species
(Figures 10–17)

Description: Shell (Figures 10–13) patelliform, of medium size for genus, up to 13.7 mm long, thick (ca. 0.9 mm above aperture margin in holotype). Outline elongated-oval, longer than wide, width 75–80% (mean 78%) of length. Profile high for genus, height 36–56% (mean 27%) of shell length. Apex heavily eroded, situated at anterior ~40% of shell length, protoconch not preserved. All slopes slightly convex. External surface whitish, sculpture consisting of thin concentric growth lines. Aperture margin concave at sides.

Soft Parts (Figures 16–17): Head rounded, stout. Cephalic tentacles short, tapering. Eyes and oral lappets absent. Foot sole large, ovate in shape, anterior pedal gland lacking, no obvious epipodium; mantle edge with numerous papillae. Ctenidium bipectinate and large. Intestine grayish in color. Gonad situated at posterior end of visceral mass. Urogenital papilla digitiform, short, with a broad, triangular base, situated right-anteriorly to visceral mass. Pericardium whitish, situated left-anteriorly to corner of visceral mass.

Radula (Figures 14–15): Formula 0+1+0+1+0. Rachidian tooth vestigial. Rachidian basal plate arched, wider than long. Lateral tooth ca. 150 μm long, with a straight, broad shaft, tip divided into three cusps. Innermost cusp outwardly bent, with a truncated tip; middle one largest, spoon-shaped; outermost one straight, with a truncated tip.

Type Locality: A methane seep area at 22°07′ N 119°18′ E, in 1120 m depth, South China Sea.

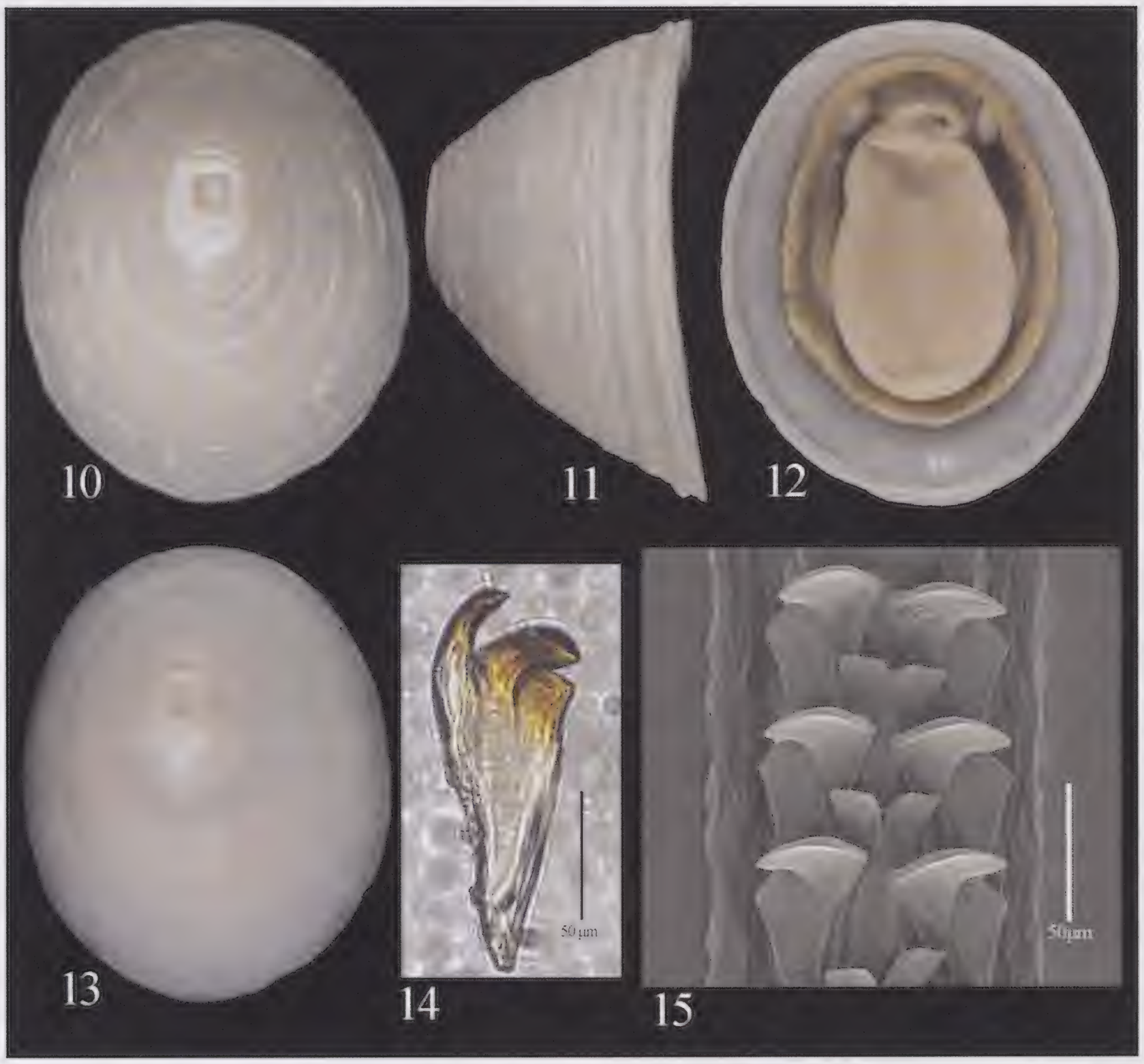
Type Material: Holotype: MBM286519, collection number: RY16123, 25 Aug. 2016; **Paratypes 1–10**, MBM286520, collected together with holotype at type locality. For measurements, see Table 3.

Distribution and Habitat: Only known from the type locality, where they were attached on black rocks and shells of *Bathymodiolus platifrons*.

Etymology: The specific epithet combines the Latin *brevis*, short, and *dentata*, toothed, an allusion to the short lateral teeth on the radula of this species.

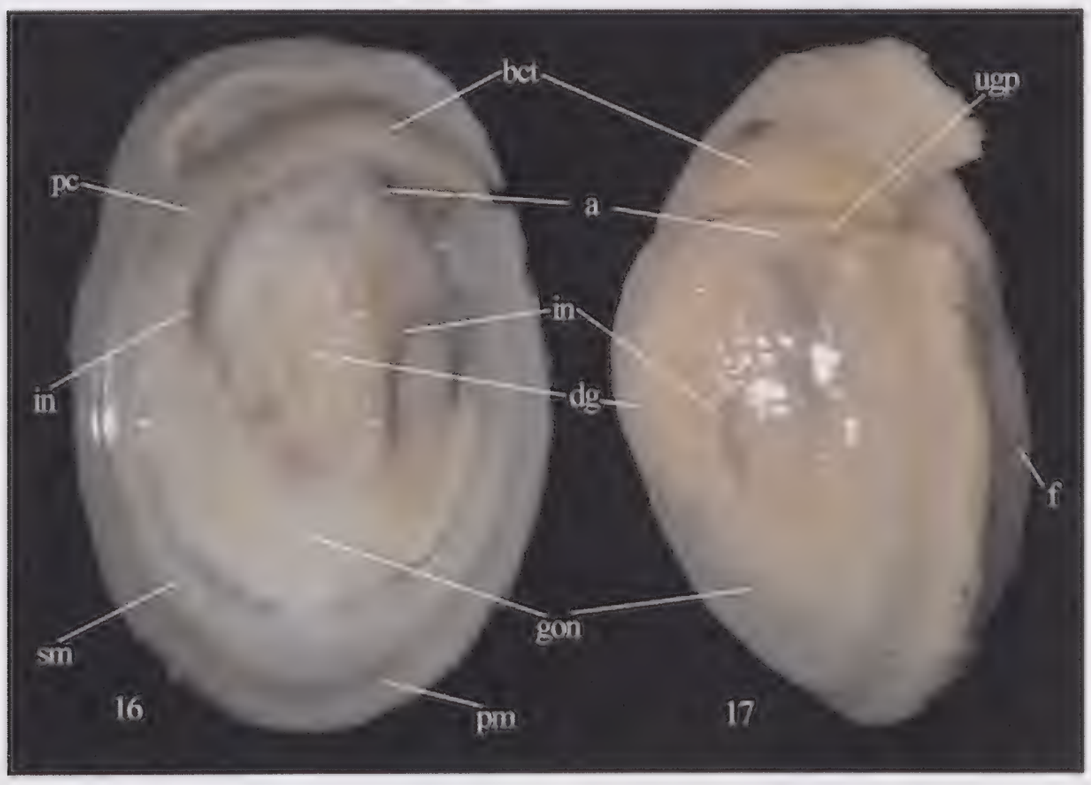
Table 3. Shell measurements (in mm) and ratios of ***Bathyacmaea brevidentata* new species**.

	Length (L)	Height (H)	Width (W)	H/L ratio	W/L ratio
Holotype	13.7	7.7	11.0	0.56	0.80
Paratype 1	12.8	5.6	9.7	0.44	0.76
Paratype 2	12.3	5.4	9.4	0.44	0.76
Paratype 3	11.5	5.0	9.0	0.43	0.78
Paratype 4	11.8	5.7	9.4	0.48	0.80
Paratype 5	11.9	5.4	9.4	0.45	0.79
Paratype 6	11.6	5.2	8.8	0.45	0.76
Paratype 7	11.4	5.1	9.0	0.45	0.79
Paratype 8	11.5	5.1	8.9	0.44	0.77
Paratype 9	10.5	4.5	7.9	0.43	0.75
Paratype 10	9.8	3.5	7.8	0.36	0.80
Average	11.7	5.3	9.1	0.45	0.78



Figures 10–15. ***Bathyacmaea brevidentata* new species**. **10–12. Holotype**, MBM286519, length 13.7 mm. **13. Paratype 2**, MBM286520, length 12.3 mm. **14–15.** Radula. **14.** Single lateral tooth under light microscope; **15.** Intact radula segment.

Remarks: ***Bathyacmaea brevidentata* new species** resembles *Bathyacmaea lactea* Zhang, Zhang, and Zhang, 2016 from the same locality in having a thick shell with thin,



Figures 16–17. Dorsal and lateral views of soft part of ***Bathyacmaea brevidentata* new species**, 8.7 mm. Abbreviations. **a:** anus; **bct:** bipectinate ctenidium; **dg:** digest gland; **f:** foot; **gon:** gonad; **in:** intestine; **pc:** pericardium; **pm:** pallial margin; **sm:** shell muscle; **ugp:** urogenital papilla.

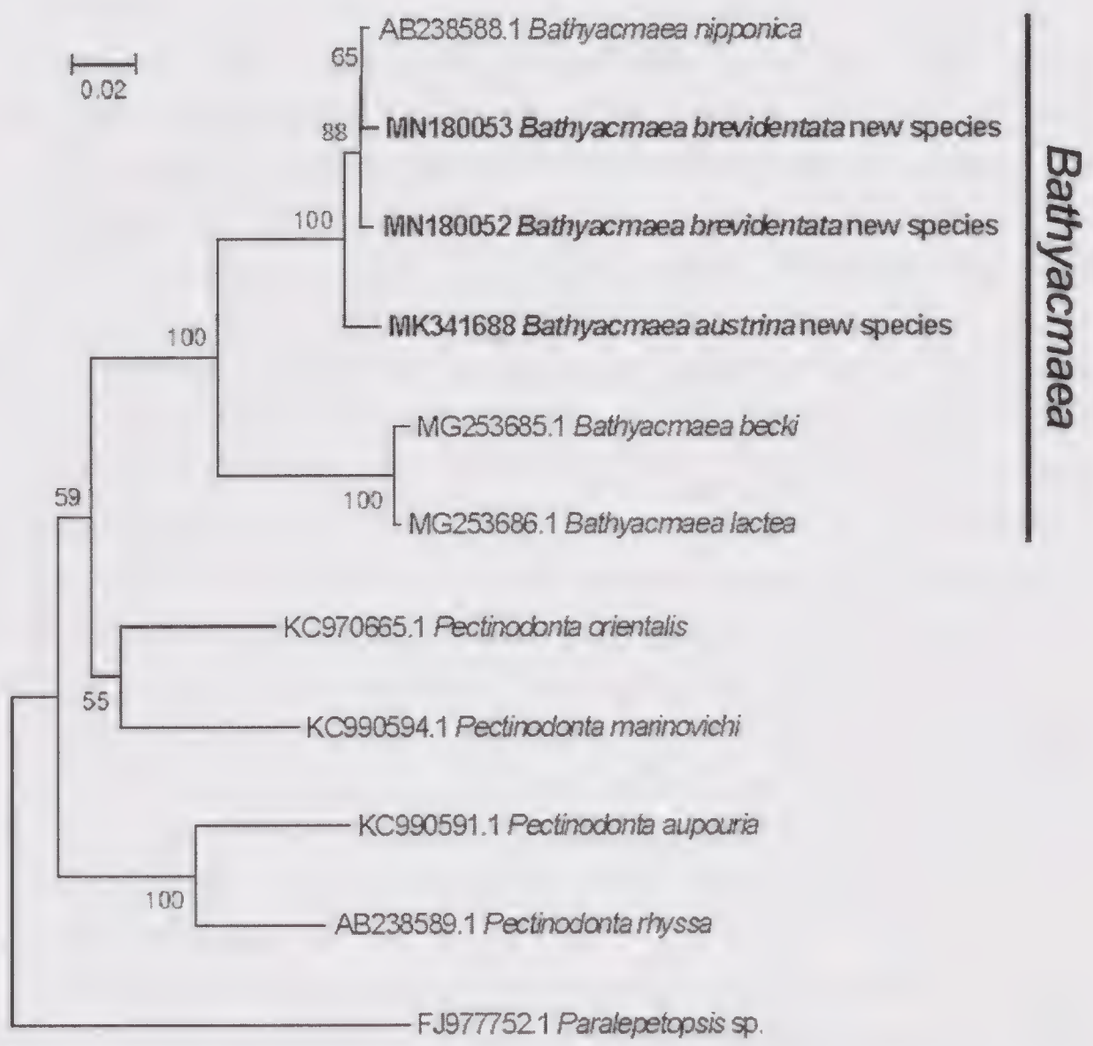


Figure 18. Neighbor-joining tree for Pectinodontidae based on suitable COI sequences from GenBank and this study. Numbers above branches indicate the bootstrap values.

regularly spaced concentric growth lines. From the new species, however, *Bathyacmaea lactea* differs in having a lower, broader shell (width/length 82–87% vs. 75–80%), and distinctive radular features (e.g., rachidian tooth represented by a longitudinal ridge, lateral tooth with much longer shaft, outermost cusp of lateral tooth with an acute tip, etc.).

MOLECULAR ANALYSES.

The NJ tree shows that ***Bathyacmaea brevidentata* new species** falls within *Bathyacmaea* in which, together with *Bathyacmaea nipponica*, it forms a well-supported sister clade to ***Bathyacmaea austrina* new species**, *Bathyacmaea lactea* Zhang, Zhang, and Zhang, 2016, and *Bathyacmaea becki* Zhang and Zhang, 2017 (see Figure 18). With available molecular data, the analysis of a 638-bp fragment of the COI gene resulted in merely a 0.6% pairwise distance between ***Bathyacmaea brevidentata* new species** and *Bathyacmaea nipponica*, whereas the pairwise distance between ***Bathyacmaea austrina* new species** and *Bathyacmaea nipponica* is 2%.Typically, the interspecific pairwise differences in COI of marine gastropods is above 3% (Meyer and Paulay, 2005). Morphologically, however, the new species are evidently different from *Bathyacmaea nipponica*. The partial COI sequence seems not to be practical for species delimitation in the genus, as in the previous case between *Bathyacmaea lactea* and *Bathyacmaea becki* (see Zhang and Zhang, 2017). These morphologically distinct species are quite different from each other, not only in shell morphology, but also in radular features, indicating that there should be sufficient generic diversity and evolutionary depth to generate such morphological differences. This requires further study to find the relevant genes.

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A new Paleocene species of *Myonera* (Bivalvia: Cuspidariidae) from eastern Hokkaido, northern Japan

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ABSTRACT

The cuspidariid bivalve, ***Myonera inouei* new species**, is described from a Paleocene (upper Selandian) calcareous concretion probably derived from the Tomikawa Sandstone and Conglomerate Member in eastern Hokkaido, northern Japan. This is the oldest record of this genus. *Myonera inouei* possibly lived in upper bathyal depths. It provides another example of taxa of deep-sea origin in the Paleocene. **The senior author, Kazutaka Amano, is the single author of the new species.**

Additional Keywords: Marine, fossil, deep-sea origin

INTRODUCTION

Deep-sea predatory bivalves of the Cuspidariidae are the most diversified group among the septibranch bivalves, and include 19 genera and 254 species (Morton and Machado, 2019). According to the previous studies, the oldest unequivocal fossil record of Cuspidariidae was a Maastrichtian species of *Cuspidaria* Nardo, 1840 (Runnegar, 1974; Heinberg, 1979) although there are some doubtful records from Triassic and Jurassic brackish sediments (Harper et al., 2002). Recently, a probably cuspidariid new genus, *Neuquemya*, has been proposed from the lower Jurassic (Pliensbachian) shallow-sea deposits in Argentina (Damborenea, 2019). From the above, it is uncertain whether Cuspidariidae had a shallow water origin or not. In her description of two new species of *Cardiomya* Adams, 1864 from the upper Eocene to lower Oligocene Keasy Formation in Oregon, Hickman (2014) discussed the radiation that Cuspidariidae has undergone in the deep sea during the Cenozoic.

Other than *Cuspidaria* and *Cardiomya*, few fossils of other cuspidariids have been recorded from Cenozoic deposits. Within the family, only two fossil species of *Myonera* have been recorded: *Myonera* sp. from the lower Oligocene Makah Formation in Washington State, USA (Goedert, 1995) and *M. osawanoensis* (Tsuda, 1959) from the lower Miocene Kurosedani Formation in Toyama Prefecture, central Honshu, Japan (Tsuda, 1959) and the middle Miocene Arakawa Formation in Saitama Prefecture, central Honshu, Japan (Kurihara, 1999).

We have found a new species of *Myonera* from the Paleocene Tomikawa Sandstone and Conglomerate Member of Tomikawa Formation (Nishijima, 1964) in eastern Hokkaido, northern Japan. We describe this new species and discuss its evolutionary significance.

MATERIALS AND METHODS

A floating calcareous concretion yielding a new species of *Myonera* was collected from a locality 550 m upstream in a small creek, a tributary of the Mokawaruppu River (43°3′36″ N, 143°40′47″ E; Figure 1). This concretion consists of calcareous sandy mudstone without any plant fragments. In outcrops around this locality, dark gray mudstone including calcareous concretions is intercalated with conglomerates. According to the geological map by Nishijima (1964), this locality corresponds to the Tomikawa Sandstone and Conglomerate Member of the Tomikawa Formation of the Nemuro Group.

Three specimens of an unknown *Myonera* species were extracted from the calcareous concretion in association with *Parathyasira* sp., *Procardia* sp., *Cochlodesma*? sp. and *Epilucina*? sp. Dinoflagellate cysts were picked from the same concretion for age determination. Taxonomic allocation of dinoflagellate cysts follows Fensome et al. (2008), where complete bibliographic references were provided. The sample was treated successively with HCl and HF to eliminate carbonate and silicate minerals. Then heavy liquid zinc bromide (specific gravity 2.0) was used to concentrate organic particles from the residues after the acid treatment.

We used digital calipers (Mitsutoyo Company, model CD-20) to measure specimens of *Myonera* species to the first decimal place. All specimens of *Myonera* species are deposited at the National Museum of Nature and Science, Tsukuba (NMNS).

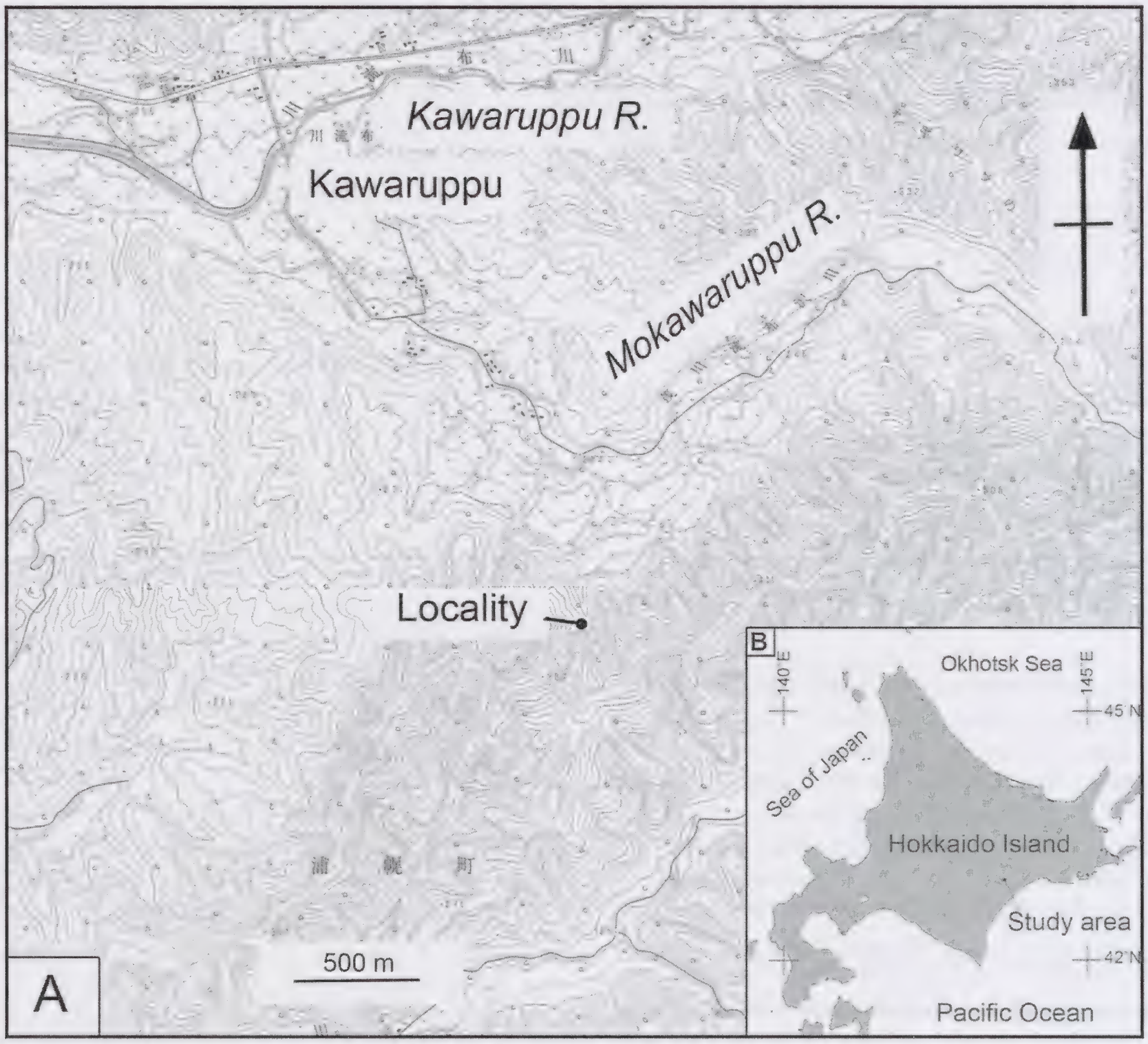

Figure 1. Locality of fossils. Base map from "Kawaruppu", original scale 1:25,000; topographical map published by the Geospacial Information Authority of Japan.

Dinoflagellate-calibrated Age of the Calcareous Concretion

The concretion yielded a number of dinoflagellate cysts whose preservation was sufficiently good for identification. Based on sixty-seven counted specimens, the dinoflagellate cyst assemblage is characterized by abundant to common occurrences of *Areoligera volata*, *Operculodinium centrocarpum*, and *Senegalinium microspinosum*, with fewer specimens of *Areoligera coronata*, *Cannosphaeropsis utinenis*, *Hystrichosphaeridium tubiferum*, *Lejeunecysta granosa*, *Manumiella rotunda*, *Palaeocystodinium golzowense*, and *Trithyrodinium evittii* (Table 1). In addition, presence of an acritarch (general name for organic-walled microfossils of apparently unicellular organisms whose biological affinity are not clear) species *Paralecaniella indentata* was also recorded. The occurrences of *Hystrichosphaeridium tubiferum*, *Palaeocystodinium golzowense*, *Senegalinium microspinosum*, and *Trithyrodinium evittii*, as well as the acritarch species *Paralecaniella indentata*, confirm correlation with the *Palaeocystodinium golzowense* Biozone defined by Kurita (2004). This zone was established in the same area in Hokkaido. According to the original age calibration (Kurita, 2004), this biozone indicates a late Selandian age. Other recorded species, including *Cannosphaeropsis utinensis*, *Lejeunecysta granosa* and *Manumiella rotunda*, are consistent with this age.

SYSTEMATICS

Family Cuspidariidae Dall, 1886

Genus *Myonera* Dall and Smith in Dall, 1886

Type Species: *Myonera paucistriata* Dall, 1886 by original designation.

Remarks: The genus *Myonera* closely resembles *Bathyneaera* Scarlato and Strabogatov, 1983 in having a rostrate shell outline and both commarginal and radial ribs. However, *Myonera* species usually has one or two strong radial ribs and a short rostrum (Krylova, 1993; Coan et al., 2000; Coan and Valentich-Scott, 2012). *Myonera* species are also similar to *Thermomya* Chen, Okutani, Watanabe, and Kojima, 2018 from a hydrothermal vent site in the southern Mariana Trough in having some commarginal ribs and a short rostrum without commarginal ribs. However, as Chen et al. (2018) pointed out, *Myonera* species have more rounded commarginal ribs and distinct radial ribs. Species in the

Table 1. List of dinoflagellate cysts and acritarchs associated with the molluscan fossils. Relative abundance of each dinoflagellate cyst taxon is expressed as VA (very abundant, 20 % and more of the total specimen count), A (abundant, 20-10 %), C (common, 10-8 %), R (rare, 8-5 %) and VR (very rare, less than 5 %).

Species	Abundance
DINOFLAGELLATA	
Achomosphaera ramulifera (Deflandre,1937) Evitt,1963	VR
Areoligera coronata (Wetzel,1933 ex Deflandre, 1937) Lejeune-Carpentier, 1938	R
Areoligera volata Drugg, 1967	VA
Cannosphaeropsis utinensis Wetzel, 1933	VR
Hystrichosphaeridium tubiferum (Ehernberg, 1838) Deflandre, 1937, emend. Davey and Williams, 1966	VR
Lejeunecysta granosa Biffi and Grignani, 1983	VR
Manumiella rotunda Wilson, 1988	VR
Operculodinium centrocarpum (Deflandre and Cookson, 1955) Wall,1967	A
Palaeocystodinium golzowense Alberti, 1961	R
Phelodinium sp. indet.	VR
Senegalinium microspinosum (Boltenhagen, 1977) Lentin and Williams, 1980	A
Spiniferites sp.	VR
Trithyrodinium evitti Drugg, 1967	VR
ACRITARCHA	
Paralecaniella indentata (Deflandre and Cookson, 1955) Cookson and Eisenack, 1970, emend. Elsik, 1977	VR

Jurassic genus *Neuquemya* Damborenea, 2019 have a small, inflated shell, a short, smooth rostrum, and some very flat radial ribs with narrow interspaces behind some commarginal ribs on the anterior half of disc. Flat radial ribs are not present in *Myonera. Neaeroporomya* Cossmann, 1886 of the family Poromyidae is similar to *Myonera* in having a short rostrum, two radial ribs and commarginal ribs on the anterior part of the disc. However, the type species of *Neaeroporomya* has an inner nacreous layer and one hinge tooth, whereas *Myonera* species lack a nacreous layer and have no hinge teeth.

Myonera inouei Amano new species
(Figures 2–4)

Diagnosis: Small *Myonera* species with a rather short rostrum; main disc sculptured with 14 to 25 raised commarginal ribs with deep, narrow interspaces; rostrum smooth, separated from main disc by sharp radial ridge.

Description: Shell small (to 8.8 mm long), elongate ovate, longer than high (H/L= 0.64 to 0.80), thin, subequilateral (AL/L= 0.44 to 0.47), subdivided into anterior main disc and rather short rostrum by posteriorly oblique, sharp radial ridge extending from beak. Antero-dorsal margin broadly arcuate; antero-ventral margin well-rounded; postero-ventral margin of rostrum slightly concave before postero-ventral corner; postero-dorsal margin nearly straight, gently sloping; posterior margin narrowly subtruncated. Surface of main disc sculptured with 14 to 25 closely spaced, raised commarginal ribs. Rostrum smooth or sculptured with a few obsolete commarginal ribs, and one weak blunt radial ridge extending from beak to postero-ventral corner. Inner ventral margin smooth. As shell material of rostrum of holotype dissolved, inner part of shell observable. Posterior adductor muscle scar rather large and elongate along dorsal margin. Pallial sinus shallow and bluntly pointed.

Holotype: Right valve (NMNS PM no. 28357), length 8.4 mm, height 5.4 mm.

Paratypes: Left valve (NMNS PM nos. 28358), length 5.5 mm, height 4.4 mm; left valve (NMNS PM nos. 28359), length 8.8 mm+, height, 6.4 mm.

Type Locality: 550m upstream of small creek of Mokawaruppu River, Urahoro Town; Tomikawa Sandstone and Conglomerate Member of Tomikawa Formation; late Selandian.

Material Examined: Three specimens from the type locality.

Remarks: The senior author, Kazutaka Amano, is the single author of the new species. Occurrences of fossil *Myonera* species are very rare. Goedert (1995) described *Myonera* sp. from the lower Oligocene Makah Formation in Washington State as the first fossil record. As he noted, this specimen looks like the Recent species *Myonera tillamookensis* Dall, 1916 (= *Bathyneaera tillamookensis*) in having at least four radial ribs on the rostrum and rough, prominent commarginal ribs on the anterior main disc. Another fossil species, *Myonera osawanoensis* (Tsuda, 1959) had been recorded from the lower Miocene Kurosedani Formation and middle Miocene Arakawa Formation, both in central Honshu, Japan (Kurihara, 1999). *Myonera osawanoensis* is characterized by a very short rostrum and a main disc ornamented with weak commarginal ribs; it resembles the Recent species *Myonera dautzenbergi* Prashad, 1932. ***Myonera inouei* new species** is the oldest record of this genus.

***Myonera inouei* new species** surprisingly resembles the Recent *Myonera angularis* (Jeffreys, 1876), which lives in deep water (530–4715m) in the North Atlantic and the Mediterranean Sea (Salas, 1996; Janssen and Krylova, 2014). The two species share a rather short as well as

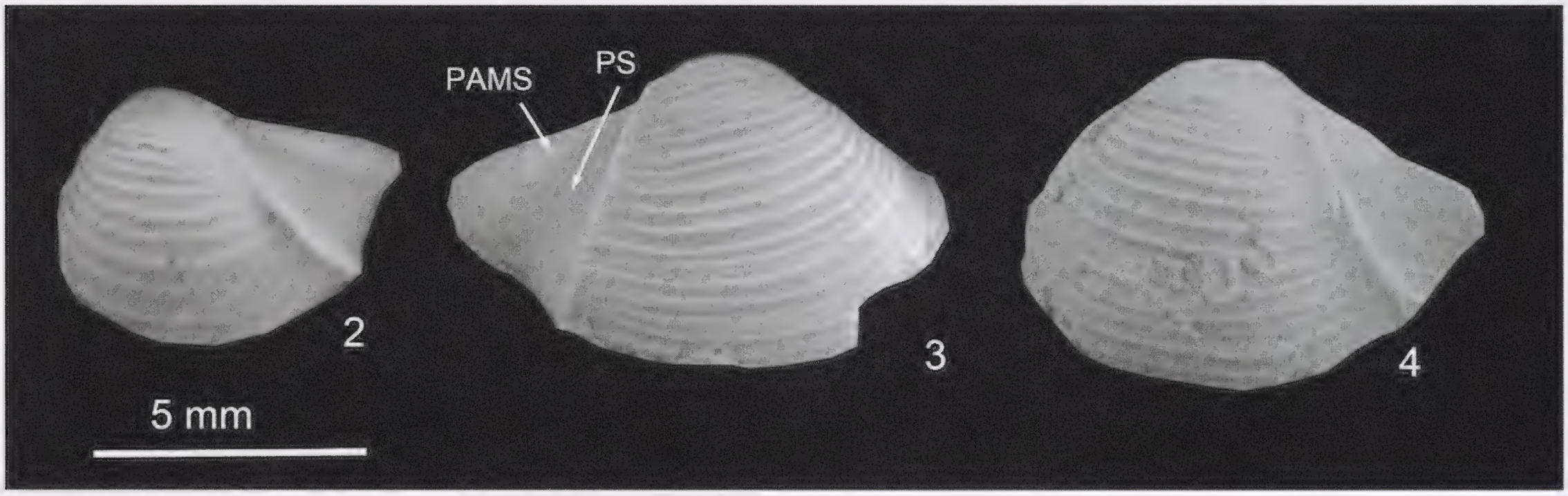

Figure 2–4. ***Myonera inouei* new species**. **2. Paratype**, left valve, NMNS PM 28358. **3. Holotype**, right valve, NMNS PM 28357; PS, pallial sinus; PAMS, posterior adductor muscle scar. **4. Paratype**, left valve, NMNS PM 28359.

smooth rostrum and many distinct commarginal ribs. However, ***Mionera inouei* new species** has a sharper ridge between the main disc and the rostrum. Moreover, the point at the end of the ridge is sharp, extending beyond the ventral margin in *M. angularis*.

***Myonera inouei* new species** is also similar to the Recent species *Myonera paucistriata* Dall, the type species of the genus *Myonera*, living in the deep water (166–3806 m) of the western Atlantic from North Carolina to Brazil and Hawaiian Islands (Allen and Morgan, 1981; Oliveira and Absalão, 2009). However, two sharp radial ribs of *M. paucistriata* easily enable us to separate from the new species.

Distribution: Known only from the type locality.

Etymology: Named for Mr. Kiyokazu Inoue in Obihiro City, who collected this species.

DISCUSSION

According to Nishijima's (1964) description and our observations, the ill-sorted conglomerates of Nishijima's Tomikawa Member can be interpreted as submarine debris-flow deposits in upper bathyal depths. The associated bivalve *Parathyasira* species now lives in depths of 50–2000 m (Higo et al., 1999). An associated Paleocene species of *Procardia* possibly inhabited the upper bathyal zone, because *Procardia inouei* Amano, 2019 was described from a Paleocene upper bathyal deposit (Amano, 2019). *Myonera angularis* which, as described above, is very similar to *M. inouei*, lives in depths of 530–4715m. Based on these data, ***Myonera inouei* new species** possibly lived in upper bathyal depths.

As mentioned above, ***Myonera inouei* new species** is the oldest-known species of this genus at present. Previously, Goedert (1995) recorded *Myonera* sp. from the Oligocene Makah Formation in Washington State as oldest-known species in the genus. However, as mentioned above, this species actually belongs to *Bathyneaera*. This implied that the oldest unequivocal *Myonera* up to now had been *M. kurosedaniensis* from the lower Miocene Kurosedani Formation. With the discovery of *M. inouei*, the fossil record of *Myonera* has been extended back to the late Selandian.

Some genera of bivalves first appeared in the Paleocene deep-water deposits in eastern Hokkaido (Amano and Jenkins, 2017; Amano et al., 2015, 2016, 2018). These are the tindariid *Tindaria*, the arcid *Bentharca*, the poromyid *Poromya*, the naticid *Neverita*, and the cancellariid *Admete*. As a result of this study, *Myonera* has been added to these genera. Our estimate is supported by the bathyal origin assessment of Cuspidariidae including *Myonera* proposed by Krylova (1989), based on the vertical distribution of the Recent cuspidariid species.

Previously, major evolution was considered to have occurred in shallow marine waters and then to have invaded deep water through geological time (Jablonski et al., 1983; Jablonski and Bottjer, 1991). However, it has recently been suggested that some deep-sea organisms such as corals, echinoderms, and mollusks originated in the deep sea and some have moved to shallow water (Pante et al., 2012; Thuy et al., 2012; Hryniewicz et al., 2017). The above six genera from the Paleocene in eastern Hokkaido support the deep-water origin theory for those organisms. Although many deep-water benthonic foraminifers became extinct at the Paleocene-Eocene Thermal Maximum (PETM) (Kaiho, 1994), some molluscs including the above six genera were able to survive the deep-sea anoxic event at the PETM.

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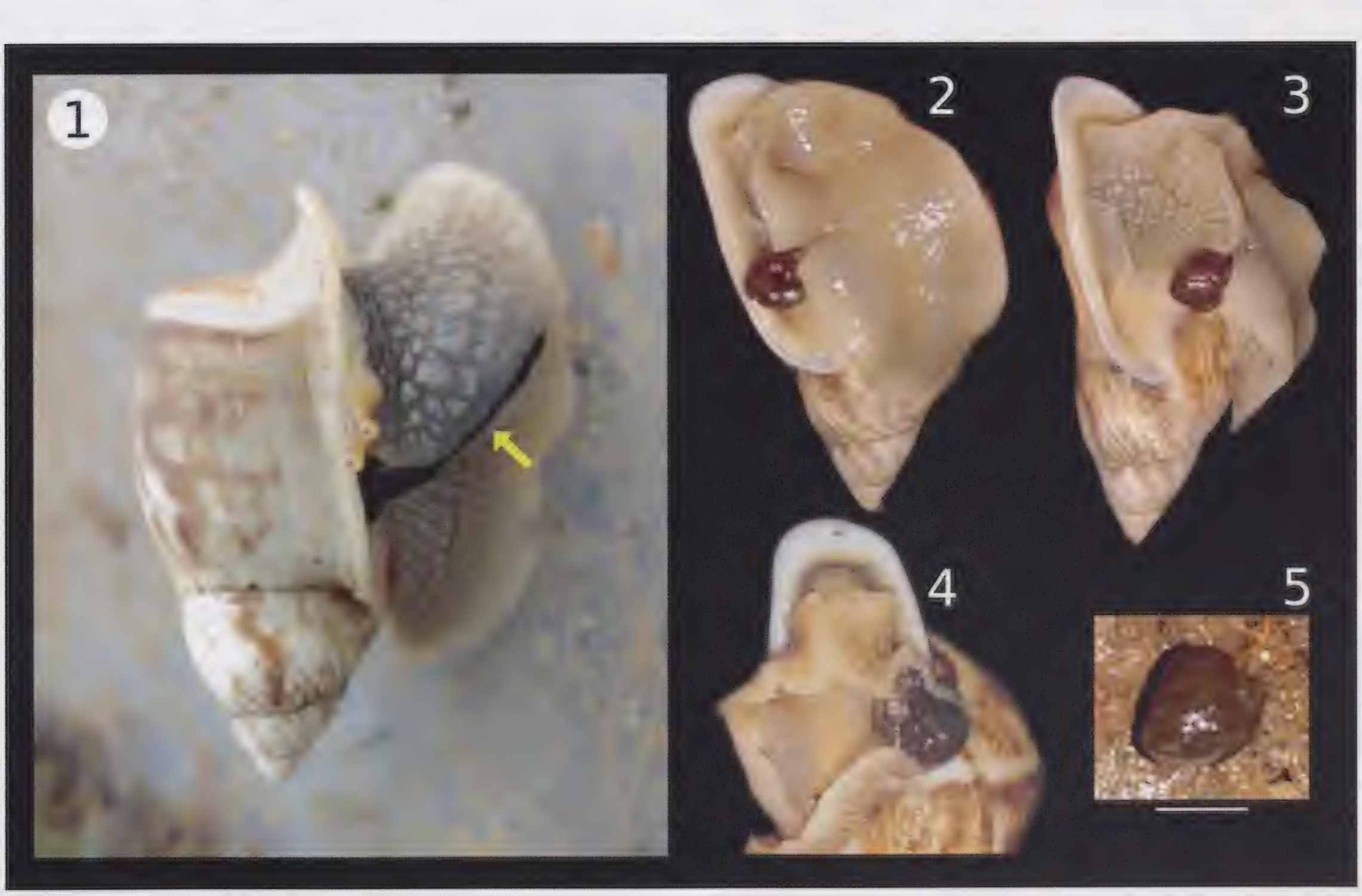
Research Note

Unusual shaping: The defecation behavior in *Cochlorina aurisleporis* (Bruguière, 1792) (Gastropoda: Bulimulidae)

Despite the perception of fecal waste as repugnant and noxious, behaviors associated with disposal of waste materials go beyond the simple elimination of unwanted metabolic residuals. The process of eliminating waste may have contributed significantly to evolutionary trends in some groups, such as the development of sociality among termites (Nalepa et al., 2001). Also, defecation behavior has important consequences for the ecological interactions in a large number of contexts: protection by discouragement against natural enemies, building structures using feces as the main construction material, frass ejection, and camouflage to blend in with the environment are some examples (Vencl et al., 1999; Weiss, 2003; Caveney et al., 1998; McMahan, 1982). Nevertheless, apart from a few studies (see Weiss, 2006 for a major revision of defecation behavior in arthropods), descriptions of this intriguing behavior have been neglected through the years and available data in literature is still scarce or entirely missing for most groups of animals.

For mollusks, there seems to be a gap in the knowledge about defecation behavior, with most studies focused on aquatic species and with an emphasis on the physiology of digestion (Lopez and Cheng, 1983), diet composition (Dekinga and Piersma, 2009), and shape of fecal pellets (Moore, 1932; Manning and Kumpf, 1959; Arakawa, 1970), with stress on the importance of fecal pellets in biodeposition (Haven and Morales-Alamo, 1966) and phylogenetic inferences (Abbott, 1954; Kornicker, 1962).

Cochlorina aurisleporis (Bruguière, 1792) is an arboreal gastropod with a purported (and unexpected) disjunct distribution: it was originally described from a bamboo forest on the island of Madagascar, but is commonly found in the Brazilian Atlantic Forest, more specifically in the states of Rio de Janeiro (Nunes and Santos, 2004), Minas Gerais and Espírito Santo (Lanzieri and Almeida, 1964). One specimen of *C. aurisleporis* was hand-collected in the



Figures 1–5. Defecation behavior in *Cochlorina aurisleporis*. **1.** Snail directing stools to the foot sole (yellow arrow). **2–4.** Shaping the fecal pellet. **5.** Fecal pellet on the ground. Scale bar = 5mm. Shell length 45 mm.

Guapiaçu Reserve (REGUA) 22°28′6.20″ S; 42°45′38.70″ W, 41 m above sea level, in Cachoeiras de Macacu, Rio de Janeiro State. The animal was kept alive for observation at the Malacological Laboratory of the Biological Institute of Federal University of Rio de Janeiro, in a 40-liter terrarium, for a period of 30 days, with leaf-litter and small tree trunks to simulate its natural environment. At an average ambient temperature of 25°C, the snail was fed lichen, fruits, and vegetables.

Contrary to the defecation process typically observed in terrestrial gastropods, where the animals just discard the fecal mass, the individual of *Cochlorina aurisleporis* directed it stool to the foot sole (Figure 1), and engaged muscle movements to shape it (Figures 2–4) into a more or less spherical fecal pellet (Figure 5). This process usually lasted for 20–30 minutes, during which the animal seemed completely concentrated, restricting body movements to the muscles around the fecal pellet. Once formed, the pellet is released, falling onto the substrate.

The potential evolutionary advantages brought by such unusual behavior are rather puzzling. It seems unlikely that the gastropod uses their own fecal pellet to achieve protection from natural enemies, such as fecal coverings, physical/chemical camouflage, and fecal shields or refuge (Müller and Hilker, 2003; Olmstead, 1994; Vencl et al., 1999). The use of the fecal pellet as a stock of resource with nutritional benefits brought by coprophagy is also unlikely. None of the pellets were observed being ingested by the animal.

Hypotethically, the use of this defecation behavior could be related to water resorption or chemical signalization. Prior (1985) demonstrated that contact rehydration in some slugs is accomplished entirely by absorbing water through the surface of the foot. Additionally, the presence of chemical compounds in feces has been described with different usages for distinct groups, including location of resting sites (Chikayoshi et al., 1974) and promotion of aggregative behavior (Dillon et al., 2000). Alternatively or concurrently, *Cochlorina aurisleporis* may use this defecation behavior as a strategy to prevent location by confusing the predators. By ensuring that their stools will be deposited far away, falling from high on the tree to the forest floor, this terrestrial gastropod with limited locomotion ability may use this behavior as a distinctive way to protect itself from chemically oriented predators.

The importance of defecation behavior for terrestrial gastropods is still poorly known and experimental manipulations are still needed to evaluate which selective pressures might have driven the unusual shaping of fecal pellets by *Cochlorina aurisleporis*.

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